ECOLOGICAL MONOGRAPHS

VOL. 18 OCTOBER, 1948 NO. 4

OFFICIAL PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA

CONTENTS

PUBLISHED QUARTERLY BY DUKE UNIVERSITY PRESS
DURHAM, N. C., U. S. A.

ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL
FOR ALL PHASES OF BIOLOGY

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Agents in Great Britain: The Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Prices can be had on application.

Entered as second-class matter December 18, 1930, at the Post Office at Durham, North Carolina, under the Act of Congress of March 3, 1879.

THE BIOLOGY OF THE WATER HYACINTH

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[1] The authors wish to acknowledge their indebtedness to the University Council on Research of Tulane University for grants-in-aid, to the United States Department of Agriculture for financial assistance during the summer of 1946, and to the New Orleans Academy of Sciences for a special research grant. They also wish to thank Dr. Walter Moore, for the determinations of dissolved oxygen, Mrs. Roberta Potts for the execution of the drawings, Virginia Minyard, Noel Ice, Jacob Kety, and Frederick Deiler for assistance in the field investigations, and Dr. Lawrence Rohrbaugh, Dr. Elwyn Hughes and Dr. Elroy Rice for painstaking reading of the manuscript.

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THE BIOLOGY OF THE WATER HYACINTH

DISTRIBUTION

The water hyacinth, *Piaropus crassipes* (Mart. and Zucc.) Britton, [*Pontederia crassipes* (Mart. and Zucc.)], [*Eichornia crassipes* (Mart. and Zucc.) Solms] is a perennial, mat-forming aquatic of wide distribution in sub-tropical and tropical regions. From all accounts it is a native of Brazil but has spread therefrom to nearly all of the South American and Central American countries. The pest now occurs in nearly all the countries in the world favorable to its development such as Australia, China, India, Indo-China, Japan, Siam and South Africa.

The accounts differ somewhat regarding its appearance in the United States. There is some evidence that it was cultivated as a greenhouse and landscape exotic shortly after the War between the States. However, the first authentic account details its introduction at the Cotton Centennial Exposition at New Orleans in 1884. Klorer (1909) states that the plant was "shown then as an exotic plant which readily made friends on account of its beautiful bloom and the little difficulty experienced in growing it. From New Orleans some of the plants were taken to the surrounding parishes and cultivated in ponds and gardens as admirable aquatic specimens. It is supposed that they were cast out or probably dumped into some nearby stream. . . ." The plant made its appearance in Florida in 1890 (Webber 1897) and has since become an important aquatic pest in that state. Shortly after the turn of the century it had been reported from all the southeastern coastal states as far north as Virginia and was reported from California by Johnson (1920).

In Louisiana there are several infested areas in the northern part of the state, particularly near Monroe and Shreveport. Although the water hyacinth extends to the Gulf of Mexico along active fresh water streams, the total amount is negligible along the coast because of its relative intolerance to salt water. It is in the area of the abandoned and current distributaries of the Mississippi River in South-Central Louisiana that the water hyacinth attains its highest development. This region of intense water hyacinth invasion extends from Point a La Hache westward to Franklin and southward from Alexandria to Houma and Point a La Hache. It includes the lower reaches of the Red River, Bayou Teche, Atchafalaya River, Bayou La Fourche, Bayou Sauvage, Bayou La Loutre, and current Mississippi deltas, as well as the fresh water lakes in the area.

DAMAGE

The annual damage done by water hyacinth in Louisiana has been variously estimated by investigators at one million to fifteen million dollars (Lynch et al. 1947). An annual loss of five million dollars would appear to be a reasonable, conservative estimate. Water hyacinth causes damage by: (1) Obstructing navigation, (2) Impeding drainage, (3) Destroying wildlife resources, (4) Reducing out-of-doors recreation, and (5) Constituting a hazard to life.

Water transportation has always been a major factor in the economy of South-Central Louisiana. Much of the produce and, in limited areas, all of the commerce, is carried along the extensive network of waterways. In addition to cotton, cane, corn, and rice, this transport includes such natural resources as fish, furs, lumber, oil, salt, sulfur, and spanish moss. The transport of these items of commerce is often delayed or prevented by the choking of streams by water hyacinth. This is true especially for citrus fruits and sugar cane and to a less extent for cotton, corn and rice.

The water hyacinth often becomes so abundant in natural streams that it impedes run-off and increases backwater and flood conditions in many areas (Fig. 1). When flood water of sufficient magnitude occur, water hyacinth is occasionally piled up on the upstream sides of bridges sufficiently to overturn them. The major but less spectacular damage occurs in connection with obstructing drainage of farmlands. In the course of about five years a drainage canal as much as 5 feet deep and 20 feet wide may be so occluded by water hyacinth that it functions poorly or not at all as a drainage canal. This aspect of water hyacinth damage is often overlooked and needs more attention if our rich alluvial lands are to continue at a high level of crop production.

A heavy incursion of water hyacinth destroys val-

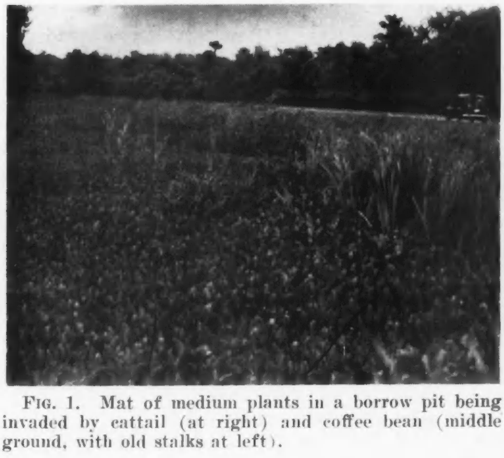

FIG. 1. Mat of medium plants in a borrow pit being invaded by cattail (at right) and coffee bean (middle ground, with old stalks at left).

FIG. 2. Channel through flotant (mat invaded by arrowhead and cattail) to permit ingress and egress of fishermen and duck hunters.

uable wildlife resources. Apparently a few water hyacinth plants in a stream, pond, or lake may promote fish production. A closed mat, however, completely eliminate all fishes except top minnows, undoubtedly due to low oxygen tensions occasioned by the decay of dead plant parts. Since water hyacinth shades out all submerged species, it eliminates many of the food plants of ducks. Furthermore, it has been shown that "rafts of water hyacinth break loose, and, driven by the wind, move back and forth in such a manner that through scouring action they tear up and destroy valuable submerged food plants" (Gowanloch 1944). The same author declared that "the blocking of water areas has quite evidently caused heavy concentrations of American coots in open water-fowl ponds so that the duck food supply of once valuable duck shooting areas has been completely consumed by coots before the arrival of the wintering duck population."

In the course of a few years streams, ponds, or lakes may be so occluded by water hyacinth as to be of no value whatever for boating and swimming. In some cases cottages have been built on bayous and lakes for recreational purposes but were abondoned due to the invasion of the water body by hyacinth. In such cases the recreational facilities of the water body were not only obliterated but the owner suffered a considerable financial loss. The shifting of water hyacinth rafts often prevents the egress of a sportsman from a recreational area. This has happened to the authors more than once. Such an event may merely result in a loss of time while fighting one's way through the block; in other cases, it may result in considerable inconvenience and discomfort, and in rare cases it may result in undue exposure, sickness, or even death. In many cases, water hyacinth rafts have reduced the landing facilities for seaplanes and constitute a hazard to takeoffs and landings of amphibious or seaworthy aircraft. In some cases aviators have mistaken green ribbons of water hyacinth for landing strips, to their own amazement, danger, and financial loss (Johnson 1920).

In at least one case water hyacinth blocked a stream carrying sewage with subsequent backing up of this material into a populated area. Last, but not least, should be mentioned the health hazard due to the breeding of mosquitoes. Although one author reported that the introduction of water hyacinth resulted in a diminution of mosquitoes, Barber and Haynes (1925) found that water hyacinth resulted in an increased production of malaria mosquitoes. They felt that the hyacinth increased malaria transmission by interfering with wave action and the activities of minnows, and also by hindering the use of larvicides and other anti-mosquito measures, including travel to mosquito-producing areas.

EXTERNAL FEATURES

The mature water hyacinth plant consists of roots, rhizomes, stolons, leaves, inflorescences and fruit clusters (Fig. 3). The roots are fibrous, unbranched and with a conspicuous root cap. They are purplish in exposed situations but white when in darkness or when rooted in the soil (Olive 1894). They vary little in diameter but greatly in length (0.3 ft. to 3.0 ft. or possibly more).

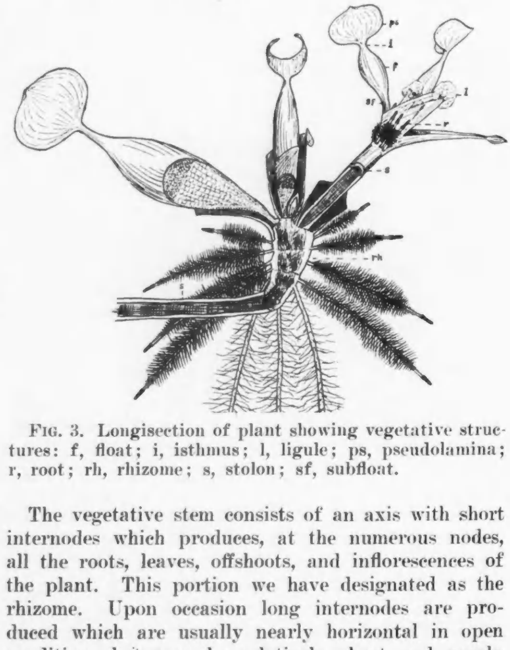

FIG. 3. Longisection of plant showing vegetative structures: f, float; i, isthmus; l, ligule; ps, pseudolamina; r, root; rh, rhizome; s, stolon; sf, subfloat.

The vegetative stem consists of an axis with short internodes which produces, at the numerous nodes, all the roots, leaves, offshoots, and inflorescences of the plant. This portion we have designated as the rhizome. Upon occasion long internodes are produced which are usually nearly horizontal in open conditions but may be relatively short and nearly vertical in dense mats (Fig. 3). In either case they produce new offshoots at their distal ends. These elongate internodes have been designated as stolons. It is very difficult in dense stands of the species to differentiate between rhizomes and stolons since. under such conditions, both are nearly vertical. However, since the two structures have quite different functions, we shall continue to refer to them as rhizomes and stolons respectively.

In general the rhizomes are 1 to 2.5 cm. in diameter and from 1 to 30 cm. in length depending on the size of the plants. The cone-shaped rhizome crown possesses a beautiful pink cap near the periphery which is about 1 cm. in length and which extends into the buds and bases of the young leaves. The reproductive portion of the rhizome tip varies in length from 1 cm. in small plants to 4 cm. in large plants. In our experiments to determine this point, we found that none of the severed rhizome tips which were shorter than 1 cm. resprouted, and none of the decapitated rhizomes produced new shoots when more than 4 cm. of the distal portion had been removed. The position of the tip of the rhizome also varies with reference to the water surface. In small plants it may be less than 1 cm. below the surface, whereas in large plants it may be as much as 8 cm. below the water line. These facts are of the utmost importance in both mechanical and chemical control methods.

The purplish stolons are similar in diameter to the rhizome, and vary greatly in length. In a closed stand of water hyacinth, they average about 2 inches long but are about 10 inches long in open stands and occasionally reach a length of 18 inches. When first produced the stolon points upward an an angle of about 60° (from the horizontal) and the roots point forward at the same angle (Fig. 3). In closed stands the stolon is so short that it maintains nearly the same position but in open stands, the stolon is soon carried to the horizontal position by the weight of the developing offshoot.

The leaf of water hyacinth has been the object of much discussion among botanists (Olive, 1894). In fully insolated plants all of the leaves possess swollen portions of the petioles hereafter referred to as floats. These float leaves consist of a membranous ligule, a subfloat, a float, an isthmus (tenuous portion between the float and the blade) and a blade (Fig. 3). According to Arber (1920) the blade is not a true lamina, but is merely an extension of the petiole. Under crowded conditions no float is produced but the petiole on the nearly vertical, equitant leaves narrows gradually from the base to the pseudo-lamina (Fig. 4). A similar type of leaf is produced on plants which become rooted on land. Since all floating plants begin their development in relatively open conditions in early spring (due to death of the former season's leaves by frost), plants collected in midseason possess float leaves on the peripheral portion and equitant leaves near the center of the leaf cluster (Fig. 4). In general the float leaves are disposed in a nearly horizontal position (15° to 45°) whereas the equitant leaves approach verticality (75° to 90°).

The stomata of water hyacinth are similar in shape, number and distribution to those of the average mesophytic, monocotyledonous plant. In appearance, the stomatal apparatus resembles the typical one usually pictured in elementary textbooks of botany. The average number (120 per square millimeter) is typical and the distribution (similar on both surfaces) is about what would be expected on an equitant-leaved plant. The stomatal apertures (12μ x 27μ) are, however, much greater than those in most plants (usually about 6μ x 12μ). The interstomatal distances are approximately 8 times the diameter of the widely open pore. From the above data it is evident that the water hyacinth, with a moderate number of very large, evenly distributed stomata, is well equipped for rapid diffusion of gases.

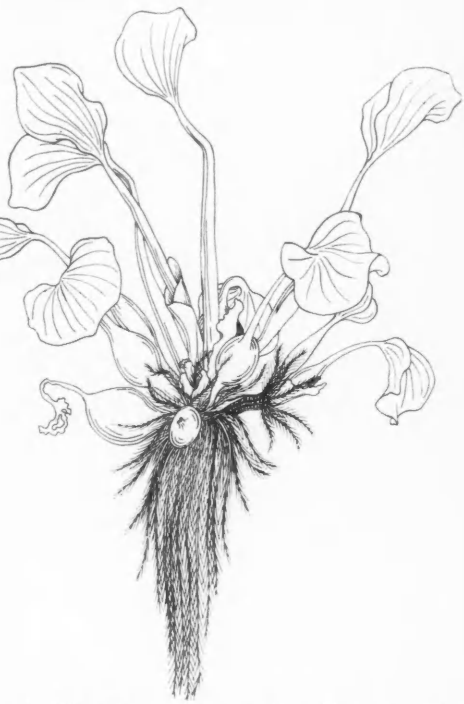

FIG. 4. Plant from dense mat in midsummer with necrotic float leaves (formed in early spring) and central, elongate leaves (formed after crowding occurred).

The most unexpected discovery in our stomatal work was in connection with leaf size. On plants which had developed on land or in poorly oxygenated water, the leaves were small and broader than long (30 mm. x 20 mm.), whereas on large plants, in flowing water, the leaves were very large and narrower than long (135 mm. x 150 mm.). Despite this very great difference in size of leaves, there were no significant differences in their stomata. Neither the number per unit area, the interstomatal distance, the size of the guard cells, nor the size of the stomatal pore varied significantly among leaves from small, medium, and large plants. This means that the greatly increased size of the leaves on the large plants is due to an increase in the number of cells and not to an augmented cell size as might have been anticipated.

The number of stomata on an individual leaf increases from the base to the tip. The subfloat lacks stomata, but the number increases rapidly from the float, (1 per sq. mm.) through the isthmus (20 per

sq. mm.) to the blade (120 per sq. mm.). It will be recalled that no floats are formed on plants growing under crowded conditions. In these leaves the transition is much more gradual. This gradual transition is more significant when it is recalled that the so-called "blade" is merely an extension of the petiole (Arber 1920).

The daily stomatal cycle does not vary greatly from the normal. Visible opening is initiated about 5 A.M., complete opening is attained slowly (not until 10 A.M.), and complete closure is effected by 5 P.M. (Table 1). It is probable that full opening does not last more than two or three hours, even on completely clear days in midsummer. On cloudy days, complete opening is rarely effected and on dark, rainy days only partial opening is attained. In many cases the stomata remain in the completely closed condition throughout the entire day.

TABLE 1. Daily stomatal cycle, June, 1946.

Hour[1]	Percent Open	Percent Partly Open	Percent Closed
12:00 Mt.	0	0	100[2]
2:00 A.M.	0	2	98
4:30 A.M.	0	7	93
5:30 A.M.	10	61	29
6:00 A.M.	42	42	16
7:30 A.M.	69	27	4
8:30 A.M.	83	16	1
9:30 A.M.	91	9	0
10:30 A.M.	100	0	0
12:30 P.M.	51	42	7
2:00 P.M.	46	43	11
4:00 P.M.	34	31	35
5:00 P.M.	1	4	95
6:00 P.M.	0	0	100
8:00 P.M.	0	0	100

[1] All hours Central Standard Time.
[2] All figures in percent, based on total number of stomata in ten high power fields.

The inflorescence of the water hyacinth is an attractive, lavender spike subtended by two bracts and surmounted on an elongate stalk (peduncle). The individual flower consists of a hypanthium, three sepals, three petals, six stamens, and a tricarpellate pistil. The pistil consists of conical ovary, a long style, and a capitate stigma which is situated about halfway between two groups of anthers. The ovary ripens into a thin-walled capsule which is imprisoned in the relatively thick-walled hypanthium. The ovary produces about 500 ovules but only about 50 seeds per capsule. The tiny seeds (0.5 x 1.0 mm.) are released by the splitting of the pericarp and the hypanthium and either are caught in the mat or sink to the bottom.

PHENOLOGY

The New Orleans area has a long frostless season (322 days) due in part to its latitude (30° North) and the warming effect (in the wintertime) of large bodies of water in the immediate vicinity. The area has no biological winter season since some plants are in bloom throughout the entire winter quarter (December 21 to March 21) and since several autumn and spring flowers have been collected on the same day (Jan. 21, 1946). During the average year, however, there is considerable destruction of the exposed parts of most herbaceous plants by frost in the New Orleans area.

In January and February of 1945 the mat was completely brown and, to the casual observer, appeared completely dead. By March 1, however, the largest leaves had attained an average length of 3.6 inches and had reached average lengths in subsequent months as follows: April, 8.6; May, 9.3; June, 14.1; July, 20.1; and August, 27.9. The greatest growth occurred from May to August at which latter time the leaves had nearly attained their maximum height. No measurable growth occurred in November or December. Growth was abruptly terminated by a moderate freeze (26° F.) on the morning of December 20, 1945. Except in protected places, apparently all the leaves in the mat were destroyed and the mat showed no trace of green to the casual observer. However, on January 27, 1946, we found that every plant possessed one or more young green leaves or green leaf bases.

In early spring rhizomes of varying lengths may be found. Apparently this is correlated with the time during the previous growing season at which the offshoot was initiated. Upon tagging a series of rhizomes, under experimental and natural conditions, we discovered a fairly uniform growth rate of 0.7 (0.6-0.9) inch per month. Our data show also that the longest rhizomes in natural mats, even at the end of the growing season, averaged only a little over 6 inches long. If this figure is divided by the average number of months in the growing season (8) we arrive at a figure of less than 0.8 inch per month. These data indicate that the rhizomes do not last very far into the next growing season. It is probable that, after a certain length has been reached, the decay at the older portion is approximately equal to the increment at the rhizome crown. If this is correct the rhizome apparently maintains a nearly constant length throughout a period of years.

In 1945, the first flowers were observed on April 1; in 1946, anthesis did not begin until April 10 and in 1947, flowering did not start until April 26. By May 1, anthesis is moderate and by June 1, maximum flowering has occurred. From June 1 to about September 1 flowering decreases and, in solid mats, is slight except along the edges fronting open water. It should be pointed out, however, that a definite rhythm of high and low flower production occurs in a given colony. This accounts for the reports of several workers that many flowers are blooming in one water body while there are few or none in similar water bodies in the immediate vicinity (Buckman 1930) and for the belief of certain workers that three or four crops of hyacinth flowers are produced each growing season. In September and October a second period of heavy flowering is ushered in and this continues through November and into December with some diminution until freezing weather supervenes.

Our experience over a three-year period indicates that anthesis is usually initiated in early April, reaches a peak in June, declines during the summer months, attains a second peak in September and early October and again declines until frost terminates flowering entirely.

ROLE IN SUCCESSION

In areas where the water hyacinth becomes established, it plays a predominant role in the aquatic fresh water sere by providing a floating platform upon which numerous other plants become established. It is believed by Russell (1942) that fresh water succession has been greatly accelerated since the introduction of the water hyacinth and the alligator weed and that "the last half century has witnessed greater changes in the Louisiana marshlands than probably took place during the twenty centuries preceding." During the past ten years the authors have kept a record of the plants which have become established on mats of water hyacinth. This list of plants included nine terrestrial, twenty-one wetland, and thirty-three aquatic species (Table 2). The species[2] list comprised nine grasses, nine composites, and seven sedges, but only two legumes. Early invaders of importance include green orchid, *Habenaria repens*, marsh pennywort, *Hydrocotyle ranunculoides*, giant smartweed, *Persicaria portoricensis*, broadleaf cattail, *Typha latifolia*, and, in places, the coffee bean, *Sesban Emerus* (Fig. 1). Two woody species (buttonball and black willow) occur on the mat but neither of these is important except in shallow water along shorelines or during the later stages of the transformation of the mat.

TABLE 2. List of species on floating mat and subsequent flotant.

TERRESTIAL	
Ambrosia trifida L.	Giant ragweed
Andropogon glomeratus (Walt.) B. S. P.	Beard grass
Baccharis halimifolia L.	Buckbrush
Erianthus saccharoides Michx.	Plume grass
Eupatorium capillifolium (Lam.) Small	Yankee weed
Rubus spp.	Blackberry
**Sesban Emerus* (Aubl.) Britton & Wilson	Coffee bean
Solidago hirsutissima Mill.	Goldenrod
Sonchus oleraceus L.	Sow thistle
WETLAND	
Carex comosa Boott	Bottle sedge
Cephalanthus occidentalis L.	Buttonball
Cicuta maculata L.	Water hemlock
Cyperus erythrorhizos Muhl.	Redroot sedge
Cyperus virens Michx.	Umbrella sedge
**Dryopteris thelypteris* (L.) A. Gray	Marsh fern
Homalocenchrus oryzoides (L.) Poll.	Cut grass
Hymenocallis rotatum Le Conte	Spider-lily
Iris giganticoerulea Small	Giant blue iris
Mikania scandens (L.) Willd.	Climbing boneset
Osmunda regalis L.	Royal fern
Phyla lanceolata (Michx.) Greene	Fogfruit
Phragmites Phragmites (L.) Karst.	Marsh cane
Pluchea petiolata Cass.	Marsh fleabane
Pluchea camphorata (L.) DC.	Marsh fleabane
Radicula palustris (L.) Moench	Yellow water-cress
Rumex verticillatus L.	Swamp dock
Rynchospora corniculata (Lam.) A. Gray	Beaked sedge
Salix nigra Marsh.	Black willow
Solidago mexicana L.	Marsh goldenrod
Verbesina alba L.	Crownbeard
EMERGENT AQUATICS	
Decodon verticillatus (L.) Ell.	Loosestrife
**Habenaria repens* Nutt.	Green Orchid
Juncus effusus L.	Weak rush
Jussiaea leptocarpa Nutt.	Primrose-willow
†*Mariscus jamaicensis* (Crantz) Britton	Saw-grass
Panicum gymnocarpon Ell.	Water witch grass
†*Panicum hemitomon* Schult.	Maiden cane
Paspalum repens Bergius	Ditch grass
Pontederia cordata L.	Pickerel weed
Sagittaria latifolia Willd.	Arrowleaf
†*Sagittaria lancifolia* L.	Beeftongue
Scirpus validus Vahl.	Giant bulrush
Scirpus californicus (C. A. Meyer) Britton	Giant bulrush
Typha angustifolia L.	Narrowleaf cattail
†*Typha latifolia* L.	Broadleaf cattail
Zizaniopsis miliacea (Michx.) Doell & Aschers.	Cut grass
FLOATING AQUATICS	
†*Achyranthes philoxeroides* (Mart.) Standley	Alligator weed
**Hydrocotyle ranunculoides* L.f.	Marsh pennywort
Jussiaea diffusa Forskl.	Water primrose
Lemna minor L.	Lesser Duckweed
Limnobium Spongia (Bosc.) L. C. Rich.	Frogsbit
**Persicaria portoricensis* (Bertero) Small	Giant smartweed
Persicaria hydropiperoides (Michx.) Small	Smartweed
**Piaropus crassipes* (Mart.) Britton	Water hyacinth
Riccia fluitans L.	Floating liverwort
Ricciocarpus natans (L.) Corda	Floating liverwort
Spirodela polyrhiza (L.) Schleid.	Greater duckweed
Wolffiella floridana (J. D. Smith) C. H. Thompson	Ligulate duckweed
SUBMERGED AQUATICS	
Azolla caroliniana Willd.	Floating fern
Cabomba caroliniana A. Gray	Carolina fanwort
Ceratophyllum demersum L.	Coontail
Potamogeton pusillus L.	Dwarf pondweed
Utricularia inflata Walt.	Bladderwort

* Early invaders; † abundant in flotant.

In the New Orleans area the typical aquatic succession in shallow ponds, lagoons, and lakes is as follows: submerged→floating mat→flotant→willow forest. The submerged community usually consists of the coontail, with or without some pondweeds. This is readily shaded out by water hyacinth. In mats of medium-sized plants of water hyacinth in stagnant water, small, nearly circular patches of dead plants often may be found. There is reason to believe that in such cases the hyacinth plants destroy themselves by interposing too large a turf of partially decayed material between themselves and the water surface. Such self-destruction is unnecessary for succession, however, since many species invade the living mat directly. Usually the mat is transformed into a flotant (floating prairie) comprising one or more of the following species: beeftongue, cattail, cut grass, giant bulrush, maiden cane, saw-grass, and water fern (Fig. 5). According to Russell (1942) the cattails do not form an effective sod whereas, the beef-tongue and the maiden cane form a firm flotant which is readily traversed by persons experienced in marshes. Excellent examples of the above types may be seen at Bay Laurent, near Des Allemands, Louisiana. In the shallower areas of flotant the willow forest ceizes readily. From our observations, however, it is evident that willows do

[2] All plant names are according to Small's Manual of the Southeastern Flora.

FIG. 5. Mat being invaded by arrowhead (left foreground) and cattail (middle ground). Walkway is about two feet above average water level. Note islands of hyacinth in pond (background).

not thrive on the highly organic substratum of the floating prairie but require a considerable amount of inorganic sediment for their successful ecesis.

The common concept of aquatic plant succession in Louisiana is that inorganic and organic sediments are deposited on the bottom until such time as the water shallows sufficiently to allow emergent aquatics, and finally wetland and terrestrial species to become established. Russell (1942) states that "while invasion is going on at the surface, a large amount of the debris becomes waterlogged, sinks to the bottom, and starts building saturated organic ooze. When the top of the ooze approaches the bottom of the mat, the way is prepared for new types of invading plants, those unable to take foothold in the mats themselves, and the establishment of typical flotant follows in short order."

Our field observations lead us to a different conclusion. In mats consisting largely of water hyacinth or alligator weed, the peaty, floating mats rarely exceed 6 inches in thickness. At this stage the bottom is barren or covered with 2 to 4 inches of soft sludge consisting of colloidal clay and partially decayed water hyacinth parts. In time (5-25 years) the water hyacinth is shaded out by alligator weed, which in turn may be eliminated by cattail, maiden cane, and marsh fern. In many cases the water hyacinth is invaded directly by these latter species. The writers studied three floating aggregations in the same borrow pit: alligator weed-cattail, cattail-marsh fern, and maiden cane-marsh fern. This borrow pit, some 30 years old, had a water depth of 10 feet at the time of our studies. In all three samples of flotant, the relatively firm, peaty mat, consisting of living and partially decayed plant parts, was 18 to 24 inches in thickness and would almost support the weight of the senior author. There were only 6-12 inches of very poorly consolidated sludge on the bottom. Although the flotant (floating marsh) was well-developed with numerous aquatic, wetland, and terrestrial species thereon, nearly 7 feet of water separated it from the sludge on the bottom. From these and other observations we believe that flotant builds from the surface downward, and not from the bottom upward.

The great buoyancy of water hyacinth is a matter of common observation. Writers have reported that water hyacinth mats often become so thick that they are able to support the weight of a dog or even a child. In several cases where water hyacinth has piled against bridges or other obstructions men have been able to walk on the water hyacinth block and in one case a cow was reported to be feeding contentedly. In order to test the loading capacity of water hyacinth a heavy wire frame was utilized. This frame was constructed of diamond-shaped, two inch, wire mesh with an area of 16 square feet and a weight of 30 pounds. In practice this was thrown on the mat and the platform was loaded with bricks until the frame was completely submerged.

An area of large plants and a plot of medium plants were selected for testing. On January 29, 1946 (the date of our first test) some leaves were completely dead and others had been killed back by frost to or part way through the floats. However, many new leaves (average of largest, 3.5 inches) had been produced by this time. Since the large plants presented a poorer mat at the start of our determinations, they exhibited a lower loading capacity as compared with the medium plants at this time (3.7 vs. 4.8 lbs. per sq. ft.). By April 13, however, the leaves of the large plants were twice as tall as those on the medium plot (12 ins. vs. 6 ins.). This resulted in a greater loading capacity in the large plants (6.2 vs. 5.4 lbs. per sq. ft.). By June 18, however, the loading capacity of both large and medium plants approximated the same figure (9.0 lbs. per sq. ft.). The loading capacity had not changed appreciably by August 13, nor was there any measurable change during the remainder of the growing season.

Preliminary observations indicated that all parts of the water hyacinth (except the seeds) floated readily. In order to ascertain the relative contribution of the vegetative organs to the buoyancy of the mat the writers determined the specific gravity of roots, rhizomes, stolons, floats, and blades by means of the volume-weight method. Volume was determined by immersing the plant parts in an Erlenmeyer suction flash and collecting the overflow in a 10 cc. graduate. It will be observed that there was little difference in specific gravity between the parts except for the floats (Table 3). The specific gravity of the floats is much lower (0.136) than anticipated and accounts for the almost fabulous buoyancy of the water hyacinth. Our data suggest the following decreasing order of specific gravities: stolons, rhizomes, roots, blades, and floats.

In order to ascertain the total material produced by the water hyacinth and invading species approximately monthly determinations of the total material were made in an 8-year-old mat over a one-year period. Each sample consisted of three cuts with a

TABLE 3. Specific gravity of plant parts.

	Mean S.E.
Root	0.782±0.045
Rhizome	0.805±0.012
Stolon	0.818±0.024
Float	0.136±0.005
Leaf Blade	0.741±0.053

sharpened, galvanized metal cylinder of 0.55 square feet cross sectional area and 3 feet in length. The material was cut out of the mat with one vertical incision and the material was "fished" out with a small rake. The material was taken to the laboratory, washed carefully, the living parts were separated from the dead remains, and the samples were dried for a week at 75° C. Although great care was exercised to obtain comparable samples in the same area it should be emphasized that a sample of 1.65 sq. ft. (3 x 0.55) can hardly be claimed to represent adequate sampling on an acreage basis.

The total weight, whether on an oven-dry weight or a wet weight basis, represents an enormous productivity per acre (Table 4), especially when one realizes that the wet weight per acre of two of our largest crop plants is much lower (corn, 15 tons, sugar cane, 25 tons) than in the 8-year-old water hyacinth mat (150 tons). It will be observed that the total oven-dry weight is relatively low in the winter and early spring but does not vary greatly during the summer months (Table 4). The relatively low total weight during the winter is due to the killing of the exposed leaves by freezing and the continuing bacterial action in the submerged portion of the mat during the so-called winter season.

TABLE 4. Plant material in a mat of medium-sized plants.

Date of Collection	Living Lbs/ Acre*	Percent Living Material	Oven-dry wt. Tons/ Acre	Wet wt. Tons/ Acre
May 6, 1945	*10,278	61	8.4	143.9
June 10, 1945	11,804	58	10.3	175.8
July 14, 1945	12,650	60	10.6	183.0
Aug. 20, 1945	11,563	65	8.9	152.2
Sept. 23, 1945	12,246	72	8.4	143.6
Oct. 24, 1945	15,600	72	10.8	184.6
Dec. 29, 1945	5,250	38	7.2	123.1
Feb. 7, 1946	3,993	27	7.4	126.5
Mar. 23, 1946	3,715	26	7.3	124.8
Apr. 23, 1946	6,487	43	7.5	128.2

*Each figure represents an average of three samples of 0.55 sq. ft. each; weight on acreage basis only approximate.

There is relatively little production of new material until April 1 and maximum total production is not attained until August 1. The percentage of living plant parts in the mat is much lower than would be expected, averaging around 30 percent during the winter and increasing to about 65 percent during the growing season.

The dry weights of all living roots, rhizomes, stolons, leaves, and inflorescences were determined from ten samples during the spring of 1946. On April 1, the leaves contributed nearly half (42 percent) and the roots and rhizomes contributed most of the remainder (52 percent) of the total oven-dry weight. By June 11, the percentage contributed by the leaves had risen to 56 percent and that of the inflorescences (from 3 percent) to 7 percent. These increases were largely at the expense of the food reserves in the rhizomes, which structures decreased from 23 percent to 10 percent in their percentage contribution.

RELATION TO HABITAT

GENERAL

The water hyacinth is equally at home in natural waters and in artificially produced water bodies. It occurs in rivers, river-sloughs, bayous, ponds, lakes, and ox-bow lakes. It thrives equally well in canals, drainage ditches, borrow pits, and impounded ponds and lakes (Figs. 1 and 2). In rapidly flowing streams it is commonly flushed out during periods of high water. It does not occur in streams or lakes with an average salinity greater than 15 percent of sea water. According to one report (Webber 1897) it does not occur in spring-fed, clear water lakes in Florida but the senior author observed it in many such lakes in the summer of 1946. After viewing almost the entire state of Florida from the air it is our feeling that many of these isolated fresh water lakes have merely escaped inoculation but are suitable for invasion by the hyacinth.

The fact that the water hyacinth can strike root and survive on land has been observed by several investigators. In protected areas along streams and in backwater areas many water hyacinth plants become stranded as much as 10 feet above normal summer river levels. On May 24, 1945, a stranded mat of water hyacinth was observed along a road embankment at Krotz Springs on the Atchafalaya River. The plants near the water line had not become rooted in the soil and could be lifted readily. Further up the bank the plants were more difficult to lift, indicating increasing root penetration with time. The plants near the upper strandage level had become firmly rooted to a depth of 4 to 8 inches with whiter and tougher roots than the water roots of the floating plants. Although the plants were deposited on a bermuda grass sod, were exposed to full insolation, and were grazed throughout the growing period, many plants survived up until October 11, 1945. Growth and flowering had occurred throughout the summer and many of the plants were still in flower at this time. These plants possessed numerous tough roots, rhizomes about 1.5 ins. to 2.0 ins. long, many (15 to 20) leaves from 2-5 inches long, and two to four inflorescences. The fresh leaves had no floats although the partially decayed, lower, and therefore, first-formed leaves did possess them. Since it is probable that the lower leaves with floats were present on the stranded plants, it is evident that these plants had survived for the entire five months

period. The lack of floats on water hyacinth plants growing on land has been noted by many writers, for example, by Spruce (1908) who wrote "when thrown on a muddy shore [they]take root there, and the swollen petioles disappear, being no longer needed."

The size of flowering specimens of water hyacinth varies tremendously with habitat conditions. The writers are suggesting the following size classes: midget, small, medium, large, and giant. The midgets are to be found rooted on land, especially along sandy or gravelly shorelines. Under such conditions, flowering specimens have been encountered with leaves three inches long and with as few as two flowers per inflorescence. Despite their size, these midgets produce normal, and apparently viable seeds. The midget and small plants rarely form a continuous mass since the midgets are found mainly on land and the small plants are encountered along the fringes or masses of larger plants. Small plants, in full flower, are often encountered in areas of shallow water grazed by cattle; in fact, our best source of flowering specimens is a shallow area which is subject to continuous grazing. Medium plants are found in water bodies with little water movement, whereas large and giant plants are encountered in moving, well aerated water of outfall canals or in the open water of ponds. Medium plants form a well-developed mat with considerable raw peat whereas large and giant plants produce poorly-developed mats with very little dead material. Medium plants flower profusely whereas large and giant plants, with leaves up to 50 inches long, rarely produce flowers or fruits. One of the most amazing discoveries was the fact that small, medium, and large plants all produced similar oven-dry weights per unit of water surface per unit of time.

In midget and small plants the flowering axes are longer than the leaves, in medium plants they are similar in length, but in large and giant plants the inflorescences are shorter than the leaves and, therefore, can be seen with difficulty. It should be reemphasized that large, and especially the giant, plants produce few or no flowers. At Bayou au Chien, Louisiana, and in the outfall canals at Belle Glade, Florida, no flowering stalks could be found except on the periphery of the plant masses. From the above it is obvious that paucity of flowering is related to large plant size. It is possible that reduced light intensity at the rhizome crown is responsible for the absence of flowering since the intensity among large plants was only about one-third that among medium plants.

LIGHT RELATIONS

Students of the water hyacinth have stated that it possesses floats only in the presence of full sunlight and in solution of high osmotic pressures. Floats are absent in dense stands, under trees, or when rooted on land. If a well-developed colony of water hyacinth is examined in midsummer, leaves with floats are evident only on the open water fringe. From the open water fringe toward the interior of a colony, the leaves change progressively from float leaves, through an intermediate type with poorly developed floats to the typical equitant leaves of the interior which possess no trace of the typical float. If plants on the interior of the colony are examined in midsummer, it will usually be found that the basal, usually dead or necrotic, leaves will possess well-developed floats and that there is a progressive change from the float leaves to the younger, equitant leaves near the center of the plant (Fig. 4). This means that float leaves are formed in early spring when full sunlight reaches the young, rosette-like plants but that equitant leaves are produced as a definitive water hyacinth canopy is developed.

In colonies with moderate-sized plants the average light value in July (average of many determinations at 8 A.M., 12 M., and 4 P.M.) was about 420 foot-candles and under a canopy of large plants the average light intensity was only 170 foot-candles. Only elongate, equitant leaves were observed in either colony. From our observations, equitant, elongate leaves are formed at intensities ranging from 130 to 500 foot-candles and float leaves are formed only when the average light intensity is above 500 foot-candles. Under a walkway of four (8-inch) boards about two feet over a water hyacinth mat, the plants under the outer boards possessed healthy, elongate leaves but those under the middle of the walkway were dead or dying, despite an average light intensity of 130 foot-candles (Fig. 5). In another experiment in which water hyacinth plants in tubs of water were placed under a table on a fire escape (average 55 foot-candles) all the plants died in two months. These observations explain why water hyacinth plants do not survive in the average laboratory (about 20 foot-candles). Perhaps they also cast doubt on the validity of much of the experimental work done on this species under laboratory conditions.

In connection with some experimental work on the relation of light intensity to the effectiveness of 2, 4-dichlorophenoxyacetic acid we attempted to determine the length of time necessary for the exhaustion of food reserves in the water hyacinth. On December 3, 1946, we selected twelve plants of similar size and age which had developed in full sunlight and placed them in darkness for 12 days. We examined two plants each at once and after 2, 5, 7, 9, and 12 days for the amount of starch present and its location.

On the day our observations were initiated, all parts of the plants possessed abundant starch with the least in the roots, intermediate amounts in the stolons, peduncles, and leaves and the greatest amount in the rhizomes. In all organs the starch grains were most numerous immediately outside each fibrovascular bundle (Olive 1894). After two days, no diminution in the amount of starch was discernible. By the seventh day, it was estimated that the amount of starch was reduced to one-half its original amount. At this time the roots were completely

devoid of starch but all other organs possessed a moderate number of starch grains. On the ninth day no starch was found in the roots, stolons, leaf blades, or peduncles although the rhizomes and other parts of the leaves (subfloat, float, and isthmus) possessed some starch. A similar condition obtained on the twelfth day although starch grains were difficult to find except in the subfloats of the leaves.

The above observations indicate that the rhizome is the main organ of starch storage and that the amount of starch diminishes with distance from this organ. It should be clear also that the dark period necessary to deplete the food reserves in water hyacinth (12 days) is much longer than ordinarily practiced in botanical laboratories (2 days). What implications these facts may have regarding the control of this aquatic pest is not clear, but it is known that water hyacinth possesses less starch in shade and is more readily killed by 2,4-dichlorophenoxyacetic acid in the shade of swamp trees than in full sunlight.

TEMPERATURE RELATIONS

When the experimental work was first started the writers placed their reserve stock of water hyacinth in tubs of water on a southwest exposure. These plants did not survive for more than a month presumably because of high water temperatures. More plants were collected and allowed to develop on a northeastern exposure where they continued to thrive throughout the growing period. In another instance two tubs of plants were placed on a fire escape on an eastern exposure on June 1. The tub farthest from the building received 5 hours of direct sunlight whereas the tub next to the building received light only for 4 hours. The plants in the tub receiving 5 hours of full sun died during July and those in the tub receiving 4 hours of direct sunlight were sickly by the end of the month. Midday (maximum) temperatures (12 M. to 2 P.M.) of water in the tubs at one inch averaged 35.5° C. and 34.5° C. respectively and at 6 inches they were the same (32° C.). Hyacinth plants do not survive in full insolation when placed in partially filled tubs or sunken pirogues or skiffs. Our observations suggest that the water hyacinth cannot survive water temperatures higher than 34.0° C. for more than four or five weeks.

The water hyacinth is rarely killed by freezing in the New Orleans area, but grows discontinuously throughout the winter. In January, 1940, however, freezing temperatures (20° F.-32° F.) were experienced on 12 successive nights and the water hyacinth was nearly or completely eliminated from many, small exposed water bodies. For example, there were few or no water hyacinth plants in Willswood Pond in May, 1940, as may be seen from an aerial photograph taken on May 8. The actual reduction of the total water hyacinth cover by the unusually cold weather of January, 1940, will never be known but estimates vary from 30 percent to 90 percent. It is reasonably certain, however, that if a concerted control campaign had been inaugurated in March, 1940, many water bodies could have been freed completely from this pest, and at slight cost.

In our experiments small water hyacinths were placed in trays with water 3 inches in depth and exposed at various air temperatures for 12-, 24-, or 48-hour periods. At an air temperature of 33° F., the blades curled, and became flaccid when placed in water at room temperatures. At or below 27° F., the exposed portions of the leaves were destroyed by the low temperatures, as indicated by blackening of the blades and upper parts of the petiole. It will be observed, however, that all plants resprouted after exposure at 27° F. and all survived when exposed at 23° F. except those exposed for 48 hours (Table 5). In all these cases, ice formed on the surface of the water and along the edge of the containers but did not form around the rhizome itself. With the 23° F., 48-hr. treatment, however, the rhizome tip was frozen and no resprouting occurred. At 18° F. the rhizome tip was frozen solid in 12 hours and the entire plant was destroyed (Table 5). These experiments prove that the rhizome tip is the vulnerable part of the plant and that the freezing of this part results in the destruction of the plant.

TABLE 5. Effect of freezing temperatures.

Temp. Deg. F.	Hours Exposed					
	Injury			Resprouting		
	12	24	48	12	24	48
33	Blades	Blades	Blades	All	All	All
27	Blades Floats	Leaves Killed	Leaves Killed	All	All	All
23	Leaves	Leaves Killed	Plants Dead	All	All	None
21	Leaves	Plants Dead	Plants Dead	Some	None	None
19	Plants Dead	Plants Dead	Plants Dead	None	None	None

Although our study is not as complete as the writers should like, it does suggest that complete destruction by freezing can be accomplished either by increasing the exposure at a given low temperature or by decreasing the temperature. Undoubtedly this time-temperature relationship could be worked out very accurately if time permitted. Suffice it to say that any freezing temperature, if continued long enough will kill the rhizome tip and that the lower the temperature the shorter the time required. Buckman (1930) feels that "temperatures much lower than 28 degrees Fahrenheit will usually kill the roots as well as the tops." Another important fact that bears on the problem is the rise of the underwater parts when the leaves are frozen and subsequently dried in the sun (Webber 1897). In general, the rhizome crown occurs at a distance of 3 (1 to 8) cm. below the water surface. When the leaves are frosted the entire mat

floats higher and when the leaves are completely removed, the rhizome crown rests at or just slightly above the water surface. At this time it is particularly vulnerable to frost since the rhizome crown is at the surface and the entire plant may be killed with even moderate, freezing temperatures in a few hours. In colder climates frosts are earlier, more numerous, and more severe. These decrease the weight of the aerial parts, elevate the mat, and thus destroy all water hyacinth plants in a short time. Our own experiments and observations, and the records of other workers in Alabama, Tennessee, and Texas lead us to believe that the water hyacinth is not becoming adapted to colder climates.

WATER RELATIONS

The water content of the hyacinth has been variously determined to be from 93 to 96 percent by various research workers. The writers determined the moisture percentage of ten plants on March 12 and found a mean water content of 96.05 (95.2-96.4) percent. These specimens were young, float-leaved plants and showed amazingly little variation in water content. The moisture percentage of each plant part (10 each) was again determined on April 1. The results (Table 6) indicate a considerable variation in the moisture percentage of the different vegetative parts. It will be observed that the rhizomes and stolons possessed the highest water content and that the leaf "blades" had the lowest moisture content (89.3 percent). The writers were particularly surprised at the relatively low water content of the roots (93.4 percent). Although it is difficult to arrive at an average water content for the plant as a whole from the moisture percentages of the plant parts, it is probable that it would be somewhat less than 96.05 percent. These results probably explain the diversity of determinations obtained by various workers since the data procured would depend on the relative percentage of the various plant parts included in the samples and the time of year when the sample was obtained.

TABLE 6. Relative percentage of water in plant parts.

Organ	Percent water (oven-dry wt.)	Percent water (fresh wt.)
Roots	1,415	93.4
Rhizomes	1,941	95.1
Stolons	2,930	96.7
Floats	1,540	93.9
Blades	834	89.3

In the growing period of 1945 a considerable variation in the contour of the water hyacinth mat was observed in a borrow pit near New Orleans. After a period of two rainless weeks there was a considerable downward slope of the mat near the shorelines whereas the middle of the mat was perfectly level. This was caused by a recession of several inches in the water level of the borrow pit. Thinking that this recession might be due primarily to transpiration, an experiment was inaugurated in early November, 1945, to determine the relative rates of transpiration and evaporation.

Twenty-two plants were placed in each of four tubs of water; water was placed in two other tubs to the same level as those occupied by the plants and two empty tubs were employed to catch rain water. All were placed in close proximity out-of-doors on the fire escape and observed over a period of five weeks. During the first two weeks the plants grew rapidly but during the next three weeks, cloudy and colder weather supervened and growth practically ceased. The total transpiration of the plants (including some evaporation from the water surface under the plants) was much greater than evaporation during the first week (2.8) and also the second week (2.9). It dropped to 1.66 during the third week and was only slightly higher during the fourth and fifth weeks (2.7 and 2.1 respectively), presumably due to the rainy, cool weather prevailing at the time.

Since the transpiration of water hyacinth undoubtedly was reduced by the cold weather during November, 1945, we decided to perform the same experiment during the midsummer of 1946. The experiment was similar except that only two tubs of 40 plants each were utilized. This number of plants gave a figure of 19 plants per square foot (827,640 per acre) which approximates that found in a dense mat at this time of the year. All tubs were placed on an open balcony, fully exposed to the sunlight until 2 P.M. after which they were in the shade of the building. At the beginning of the study, on June 17, the largest leaves were 12 inches long, but they had grown to a length of 20 inches by July 20 when the experiment was terminated.

Because of the increasing total leaf surface, the total transpiration per tub of plants per unit of time increased throughout the experiment (Table 7).

TABLE 7. Transpiration in relation to evaporation.

Date	Conditions	Total transpiration, Milliliters	Evaporation, Milliliters	Transpiration / Evaporation
June 17-June 19	Clear	8,650	1,900	4.5
June 20-June 28	Cloudy, rain	27,400	10,500	2.6
June 29-July2	Clear	11,700	2,800	4.2
July 3-July 9	Cloudy, rain	26,900	13,200	2.0
July 10-July 20	Clear, except 13th, 14th	31,700	4,800	6.6
Total	Clear, 13 days; Rain, 21 days	106,350	33,200	3.2

During the first few (sunny days) of the experiment the water level in the tubs with plants dropped much faster (more than 1 in. per day) than in the evaporation tubs. This was reflected in the relatively high total transpiration-evaporation ratio of 4.5 (Table

7). During the period from June 20 through June 28, a total of 4.69 inches of rain was recorded. During this period the total transpiration was relatively low and was only 2.6 times the evaporation (Table 7). During the next 4 days the total transpiration-evaporation ratio climbed to 5.9 and was still higher (6.6) during the relatively sunny, hot period from July 10 through July 20. Over the entire period of 34 days, the transpiration averaged 3.2 times the evaporation. The relatively high total transpiration-evaporation ratios are to be explained primarily on the basis of the much greater evaporating (transpiring) surface of the plants as compared to the open water. Our data lend support to the concern of agriculturists in Florida, Texas, and California who have become interested in water hyacinth removal because they use up irrigation water.

In one mechanical control operation the engineers utilize the principle of depositing water hyacinth plants on relatively dry banks. To determine the capacity of this species to survive desiccation we deposited plants on a galvanized metal surface, on grass in an open lawn, and in the shade of shrubbery at the edge of a lawn. We exposed many weighed plants for varying periods under the above conditions, after which the plants were reweighed and placed in tubs of water in partial shade to determine survival.

In general, water hyacinth plants survived as follows:

1. Sunny weather, galvanized metal, 1 day
2. Sunny weather, open lawn, 6 days
3. Cloudy and rainy weather, open lawn, 12 days
4. Sunny weather, shade of shrubs, 8 days
5. Cloudy and rainy weather, shade of shrubs, 18 days.

The causes of the death of exposed plants apparently varied somewhat depending upon the environmental conditions. In the case of the plants placed on the galvanized sheet metal, the writers believe that the cause of death was excessive heat. The metal was unbearably hot to the hand, the floats were obviously scorched and the exposure weight, much higher than that of plants which survived on the open lawn, was 22 percent of original weight. In the case of the specimens on the open lawn desiccation was probably the primary cause of death. In water hyacinth, death usually occurs when the weight of the exposed plants falls below 15 percent of its initial wet weight. In the shade plants, desiccation appears to be the main cause of destruction during the sunny period but fungi and sowbugs were contributing factors during the inclement period, since petioles were still green, rotting was evident, and the percentage of moisture was still above the critical point for survival.

When the plants, which had been destroyed in those experiments, were removed from the tubs, superficially dried, and reweighed, it was found that they returned to, or even above, their initial wet weight. They remained afloat for the duration of the experiment (three weeks). This checks with field observations that plants which are destroyed by cutting, or spraying with arsenicals or formagens, remain afloat for six weeks or more.

In the autumn of 1945, the water level dropped sufficiently to allow most of the water hyacinth plants in the northern end of Waggaman Pond to become firmly attached to the soil. When the winter rains came, the majority were completely covered with water and remained in the submerged condition nearly continuously from December onward. It was our feeling that these plants would survive readily since they would be well protected from low winter temperatures. All the plants died, however, probably due to lack of oxygen, and the area (of several acres) was almost completely devoid of water hyacinth in early April.

In August, 1946, the water level again dropped to such an extent that nearly all the plants at the northern end of Waggaman Pond became rooted in the mud. With abundant September rains many of these plants, especially along the road fill, were covered with water. Instead of remaining on the bottom, however, these plants produced an abscission layer across the rhizome just below the lowest living leaves and floated to the surface about ten days after submergence. Examination of the plants showed that the previous root system was left behind, that young roots had appeared just above the abscission layer before the rhizome had been abcised, and that continuing root production occurred after the plants reached the surface. In this case, death by suffocation did not occur since the formation of an abscission layer allowed the plants to float to the surface.

By a simple experiment it was discovered that seedlings behaved in a similar fashion. In this experiment fragments of the mat with either strap-leaved seedlings (30 days old) or float-leaved plantlets (60 days old) were placed in finger bowls with an open web of strings across the top. This web prevented the mat from floating upward but permitted detached seedlings to rise to the surface. The units (in duplicate) were submerged in tubs of water and observed for 40 days. As in the case of mature plants, these seedlings formed an abscission layer across the young rhizome, formed roots just above the abscission zone, became detached from the former root system, floated to the surface, and continued their development as floating plantlets (Robertson and Thein 1932). The float-leaved individuals began to appear at the surface in 10 days and all were at the top in 40 days. In contrast the strap-leaved seedlings did not appear at the surface until 20 days had elapsed and did not complete their detachment by the end of the experiment (40 days). Upon examination it was discovered that these seedlings rarely came to the surface until they had developed float leaves. The results of this experiment indicate that seedlings not only sever themselves from their former root system, but also that they are able to withstand submergence for at least 40 days and to develop new float leaves while still in the submerged condition.

Upon occasion it has been the practice to pile water hyacinth plants inside a pen in deep water to effect their destruction. It was noted that some of the submerged plants, not covered to any degree by other plants, survived for long periods. To determine the effect of submergence, we placed 26 young, healthy plants in a tub, confined them within a wire mesh screen and submerged them by placing water-filled glass containers on the screen. This condition allowed light and dissolved gases to pass down to the plants with little hindrance. Since water temperatures range from 55° F. to 70° F., the conditions for survival were rather favorable.

In general, all plants showed the same characteristics at the end of 6 days: exfoliation of older parts of rhizomes and of young offshoots (when present), increasing paleness and length of leaves, considerable compression which did not increase after the sixth day, epinasty which increased up to the twenty-fourth day, and necrosis which appeared about the sixth day and continued to the end of the experiment (Table 8). Two facts are noteworthy. Epinasty occurred here as it has in all cases where the seedlings or mature plants have been confined for several hours in covered containers, leading one to suspect that poor oxygenation, in air or in water, may be a factor in inducing epinasty. The survival of water hyacinth plants, or their offshoots, for such long periods of time under water is surprising in view of the aerial habit of their leaves and flowers. It is probable that the period of survival would have been reduced under field conditions during the hot, summer period. The above experiment does emphasize, however, the very high survival capacity of this species.

EFFECTS OF SALINITY

Certain research workers have indicated their belief that the water hyacinth is adapting itself to salt water. The writers noted floating water hyacinth plants in Lakes Pontchartrain and Borgne but never in protected areas except near entering fresh water streams. However, they were found in considerable numbers rooted along the shorelines of both of these lakes. In their work on the marshlands of Southeastern Louisiana, Penfound and Hathaway (1938) cite the water hyacinth and tupelo gum as the best site indicators for the fresh water habitat. They state that water hyacinth does not ecize in even faintly brackish (sawgrass) marsh. The writers have examined several areas and found this still to be the case. It has been pointed out by one worker that fresh water currents often occur well out in saline lakes since the fresh water remains on the surface for long periods. This phenomenon accounts, in part, for the presence of water hyacinth plants a considerable distance from the shoreline of salt water bodies.

In the autumn of 1945, a large sample of salt water was collected from Mississippi Sound. This water (1.2 percent salt) was mixed with tap water to give salinity percentages as follows: 0.6, 0.3, 0.15, and 0.08. Ten water hyacinth plants each were grown in these concentrations for 8 days. Only the plants in the two higher concentrations (1.2 and 0.6 percent) were dead at the end of the experiment. A similar experiment was conducted in July, 1946, using water from the Gulf of Mexico. This water (2.0 percent salt) was mixed with tap water to give percentages as follows: 1.0, 0.5, 0.25, 0.12, and 0.06. Five water hyacinth plants were grown in each of six tubs containing water of the above concentrations. Water was added as necessary to bring the saline water back to the initial concentration.

For the first 6 days the results were similar to those in 1945, but the more interesting and significant results were obtained in the last 22 days of the experiment. Although the experiment was discontinued after 28 days, it was obvious that all the plants at all concentrations, except at the weakest one (0.06 percent salt), would have died in a few more days (Table 9). At the 2.0 percent salt concentrations the plants were killed by wilting and crisping so rapidly that epinasty was not observed. At all other concentrations the usual sequence was as follows: epinastic curvature of leaves to or below the water surface, chlorosis, and finally necrosis of

TABLE 8. Effect of submergence on development and survival.

Days Submerged	Characters Observed	CONDITION, AFTER REMOVAL TO NORMAL CONDITIONS			
		0 Days	6 Days	12 Days	18 Days
6	Color	Lighter green	Normal	Normal	Normal
	Epinasty	Slight, +10°	No change	No change	No change
	Necrosis	None	None	None	None
15	Color	Very pale green	Light green	Normal	Normal
	Epinasty	Great, −20°	No change	No change	No change
	Necrosis	Blades 10%	20%	40%	Blades, 50%
27	Color	Pale, elongate	Pale green	Pale green	Light green
	Epinasty	Great, −40°	No change	No change	No change
	Necrosis	Heavy, 25%	50%	65%	75%
39	Color	Pale, elongate	Pale, elongate	Pale green	Pale green
	Epinasty	Great, −40°	No change	No change	No change
	Necrosis	Heavy, 50%	Old plants rotted, new plantlets healthy		

the plant parts in contact with the water. It should be noted, that, at most concentrations, flaccidity or wilting did not precede the death of the plant parts and that necrosis occurred primarily when the plant part was in contact with the water surface. One research worker states that by splashing water over hyacinths by speed boat in fairly brackish waters it was possible to hasten the destruction of this species. These experiments prove, beyond question, that the water hyacinth is a fresh water plant and cannot tolerate more than faintly brackish water.

TABLE 9. Effect of salinity on survival.

Days Exposed	Observed Phenomenon	PERCENT OF SALT					
		2.0	1.0	0.5	0.25	0.12	0.06
2....	Crisping	Heavy	Slight	None	None	None	None
	Necrosis, %	50	25	10	Slight	None	None
7....	Epinasty		Marked	Slight	None	None	None
	Necrosis, %	100	80	25	10	None	None
14....	Epinasty		Marked	Marked	Marked	Slight	None
	Necrosis, %	100	95	80	50	20	5
21....	Epinasty		Marked	Marked	Marked	Marked	Slight
	Necrosis, %	100	100	90	60	40	10
28....	Epinasty		Marked	Marked	Marked	Marked	Marked
	Necrosis, %	Discarded	100	95	80	50	20

REACTIONS ON PHYSICAL FACTORS

A moderate water hyacinth infestation causes relatively little change in the habitat conditions of an area. With complete coverage, and especially when a dense turf or raw peat is formed, the changes in physical factors are profound. If the habitat conditions under a closed mat of water hyacinth be compared with those in open water, the surface water temperature is more uniform, the acidity is higher, the carbon dioxide tension is higher, and the amount of oxygen in the water is much lower (Lynch et al. 1947). On an average the pH of the bayou, canal, and pond waters in the Mississippi River Delta is about 7.2 whereas the water in or near mats of this species are usually acid (pH 6.2-6.8).

Altogether the writers have made 28 determinations on oxygen tensions in all sorts of situations. For the sake of uniformity of presentation the oxygen tensions will be considered at the level at which most of our determinations were made (6 inches below the water surface). In general, the oxygen tensions under heavy mats (with about 4 inches of decaying peat) were less than 0.1 part per million (ppm.). With closed mats, but without the peat it was usually about 0.5 ppm., in open mats (up to 80 percent cover) it averaged about 1.5 ppm. and in open pools and ponds it was about 4.0 ppm. Certain exceptions should be emphasized. In pools which were cut in dense mats the dissolved oxygen was always low (usually less than 1.0 ppm.). This was true also in the open water of bayous and canals downstream from dense mats. On the other hand, oxygen tensions were relatively high in the interior of mats downstream from the open water of canals, ponds, or irrigation lakes. In open pools in the mat which were blanketed with *Azolla*, *Lemna*, or *Spirodela* the oxygen tensions were usually below 1.0 ppm.

An experiment was initiated on November 14, 1946, to determine the relative capacity of water hyacinth parts to lower oxygen tension. One and one-half pounds each of roots, stems, leaves, and spent inflorescences were placed in tubs containing 8 gallons of water. Water was added weekly to bring to the original level. Periodic observations were made on the necrosis, decay, and position of plant parts as well as the temperature and oxygen tension (3 inches below the water surface). Decay of parts occurred in the following order: roots, inflorescences, stems, and leaves. By the seventh day the roots were largely submerged and distributed evenly throughout the water, the inflorescences were on the bottom but the stems and leaves were still at the surface.

The leaves had not reduced the oxygen tension below that of the control (without plant parts) by the seventh day. This was due to the fact that the leaves had experienced very little decay. At the next sampling (24 days later), however, the dissolved oxygen under the floating mat of decaying leaves was very low (Table 10). It will be noted that the lowest dissolved oxygen was obtained among the roots on the seventh day and that the oxygen tension in this tub rose throughout the experiment (Table 10). This was attributable to the gradual sinking of the roots and the subsequent diffusion of oxygen from the air into the free water above the root mass on the bottom. In the above experiment the low oxygen tensions obtained were due to decaying parts but only when these parts were at or near the surface of the water. There is no significant difference between the plant parts of water hyacinth in lowering oxygen tension. It is probable also that the decay of any other free-floating species would result in a similar decrease in oxygen tension.

The water hyacinth parts were left in the tubs to determine the rapidity of decay. Since the oxygen tensions were known to be fairly high when the plant parts were on the bottom, it was anticipated

TABLE 10. Relation of decaying plant parts to dissolved oxygen.

Days from initiation	DISSOLVED OXYGEN, PARTS PER MILLION				
	Roots	Stems	Leaves	Inflorescences	Control
7........	0.4	5.7	7.8	6.5	8.8
31........	1.4	4.0	1.4	5.0	7.7
57........	5.3	5.2	2.2	7.1	6.5
134........	6.0	5.4	6.5	7.3	6.5

that decay would be relatively rapid with the advent of hot weather in the summer of 1947. However, it was estimated that less than half the original material placed therein on November 14, 1946, had disappeared by July 1, 1947. On July 28, the wet weights of the residual material was determined with the following percentages of the original materials: roots, 55; stems, 46; leaves 30; and inflorescences, 42. It is probable that decay would be less rapid under hyacinth mats, because of low dissolved oxygen, than under the above experimental conditions. If true, it is obvious that the presence of dead hyacinth parts might interfere with the ecesis of submerged aquatic plants and the spawning of fish for months or even years to come.

The experiments, as well as the field data, of the writers indicate that the water hyacinth is a potent biotic factor in lowering the oxygen tension in the fresh water bodies in Louisiana. Since relatively few fish (for example bowfin and gar) can tolerate oxygen tensions as low as 1 p.p.m., it is obvious that most fish will be excluded from waters that possess closed mats of this plant (Lynch et al 1947). It should be obvious also that the water hyacinth constitutes an ever present threat to the fisheries resources of the fresh water areas of Louisiana.

VEGETATIVE REPRODUCTION

The relatively rapid rate of colonization by water hyacinth has been noted by many writers (Buckman 1930; Spafford 1935), the statement often being made that a mat migrates at the rate of about three feet per month by vegetative propagation. On May 10, 1947, the edges of two stands (12 ft. x 15 ft.) of water hyacinth were trimmed and the migration rate determined. During the first month the average extensions from the periphery of the stands were 2.2 feet and 1.6 feet respectively. For the period of observation (May 10 to Oct. 10) the average monthly rates for the two stands were 2.2. feet and 1.9 feet respectively, an average of about 2 feet per month. Since only the central, and deeper part of a bayou is cleared for navigation, this means that the migration inward (from both fringes), would be 4 feet per month. Actually the migration rate in bayous is somewhat greater than this since fragments, which are often detached from the mat, present an increased periphery for migration.

Six field experiments have been carried out regarding the rapidity of vegetative reproduction in the water hyacinth. A plot 12 ft. x 15 ft. in an area free of water hyacinth was made by constructing a barricade of willow branches. Ten healthy plants were placed in this area on March 4, 1946. Multiplication by offshoots was very rapid, the rate of doubling varying from 11 days to 18 days, depending on the weather (Fig. 6). By June 4, 1946, (3 months later) the pool was filled with plants (1,610) and flowering had been initiated. In this experiment, the number of plants doubled every 12.5 days. This same experiment was duplicated later in 1946 and twice in 1947, the rate of doubling varying from once every 11.2 days to once every 15.0 days. If now an average rate of doubling of once every two weeks and a growing season of 8 months is assumed, then 10 plants, given plenty of room and good growing conditions, would produce 655,360 plants (a solid acre of water hyacinth). These figures emphasize, in a dramatic manner, the fantastic colonization rate of this species and the necessity of early treatment, continuing vigilance, and retreatment with a view to complete eradication in areas where control has been inaugurated.

FIG. 6. Colonization pool, eight weeks after 10 plants were placed therein.

The writers wish to present one notable exception to the rapid rate of colonization by this species. On April 21, 1945, a pool of 9 ft. by 9 ft. was made in a water hyacinth mat in a borrow pit ten miles west of New Orleans. Eight plants were placed in the pool. During the first month the introduced plants were sickly and had only increased to a total of 20 plants. Colonization proceeded slowly for the rest of the season with total plants as follows: Third month, 33; fourth month, 46; and fifth month, 63. This means that the rate of doubling was only once every 50 days, about one-fourth the rate described above. At the end of our observations, on September 23, 1946, the total cover was still only 55 percent of the pool surface. The oxygen tension averaged only 0.8 p.p.m. in this pool whereas that in the pools with rapid colonization ranged from 3.5 p.p.m. to 4.8 p.p.m. Low oxygen tension, therefore, was undoubtedly responsible for the poor health, the poor vegetative reproduction, and the slow colonization rate of water hyacinth in this pool.

In the past few years segmenting the mat in place has been used extensively as a control method. However, the segmented material from these machines (locally called saw-boats) resprouts abundantly (Table 11) and some of it remains afloat for 6 months. Simple experiments were devised to determine the reasons for the low efficiency of these machines and, if possible, to improve their performance. In our first experiment, however, we became very

TABLE 11. Effect of segmentation on regeneration.

Days after segmentation	Percent of plants resprouting			
	Cut by Saw-boat	Cut Only	*Cut, sprayed	†Cut, Piled
20..........	70	42	40	10
50..........	75	49	48	17

*With 2, 4-D at 1 lb. per acre immediately after segmenting.
†Cut material from one plot piled on another segmented plot.

discouraged since the bisecting of 10 rhizome crowns resulted in the production of 20 new plants. Subsequent experiments were not quite so discouraging, however. A segmenting apparatus, consisting of a square foot frame with knives set one inch apart, was constructed. With this apparatus it was possible to segment one square foot of the mat at a time, similar to the action of the saw-boats, and by turning at right angles, to chop this part of the mat into fragments one inch square. In practice one square yard plots were segmented and left in place for subsequent observations.

In all cases most of the cut material floated throughout the course of the experiments (50 days). The percentage of the rhizome crowns resprouting was somewhat less in our segmented plots than the material from the saw-boats (Table 11). Spraying the freshly cut material with the sodium salt of 2,4-dichlorophenoxyacetic acid did not affect the rate of regeneration. This means that it would be useless to spray the freshly segmented material from saw-boats. When the cut material from one plot was placed on the segmented plants of another plot, the percentage of the total rhizome crowns which resprouted was very low (Table 11). This checks closely with the observations of field workers that piling results in a greatly decreased resprouting of the cut material. This is probably due to the actual blanketing of rhizome crowns as well as the creation of poor growing conditions in the putrescent mass.

The crusher has proven very effective in destroying water hyacinth but cannot be operated in shallow water (Wunderlich 1938). Crowns of crushed water hyacinth from the crusher U.S.S. Kenny were obtained on September 6, 1946. Ten each were placed in large battery jars nearly filled with water and their subsequent history was observed. In three days an oily film appeared on the water surface, indicating some putrefaction. The water became progressively more putrid during the period of the experiment (18 days). No sign of regeneration of any of the 20 specimens occurred throughout the observation period. This experiment demonstrates beyond question the efficacy of crushing as a means of destroying water hyacinth.

SEXUAL REPRODUCTION

Floral Structure

The inflorescence of the water hyacinth is one of the most interesting objects in nature. It consists of an erect, naked axis, hereafter referred to as the peduncle, surmounted by two bracts which subtend the actual flower cluster. The lower bract possesses a blade but the upper, innermost, and slightly shorter bract is bladeless. The portion of the axis, immediately above the bract, but which bears no flowers, has been designated as the subrachis, whereas the flowering portion distally has been referred to as the actual rachis. The rachis bears a variable number of flower buds, or flowers, set in relatively deep pockets arranged spirally.

The individual sessil flower faces outward from the spicate inflorescence. It consists of a hypanthium, a perianth of three separate sepals, and three distinct petals, six stamens and a tricarpellate pistil (Fig. 7). The hypanthium is about 17 mm. long and curves gradually away from the axis of the rachis. The general color of the perianth varies from pale to deep lavender (pale-purple) but the banner petal possesses a diamond-shaped chrome yellow (yellow-orange) spot surrounded by a wide pale purple-blue border. The sepals are very similar in size, although the side sepals are somewhat longer. On the other hand, the corolla shows considerable zygomorphy. On most flowers the androecium consists of three short stamens (8 mm.) and three long stamens (22 mm.). The filaments are white at the base but deep-purple distally, are beset with diamond-like, glandular hairs, and bear attractive violet anthers. The anthers average 1.4 x 2.2 mm. and contain about 2,000 pollen grains each. These grains are oval, reticulate, monocolpate and relatively large. When dry the pollen grains average 32 mm. x 69 mm. but are considerably wider when moist (55 mm. x 69 mm.). The pistil consists of an obtusely conical ovary, a long, white to lavendar style with jewel-like, glandular hairs, and a white, capitate stigma. The ovary produces about 500 ovules but rarely sets more than 50 seeds per capsule.

FIG. 7. Flower of water hyacinth. Left: longisection, showing hypanthium, long and short filaments, and medium style; right: face view.

In general, the length of the style is such that the stigma is brought into an intermediate position between the two groups of anthers (Fig. 7). In two groups of plants, one in Louisiana, and another in Florida, however, flowers were observed with short and medium filaments but long, reddish-purple styles. Perhaps a third type of flower with short styles,

medium filaments and long filaments should be expected but the writers have never encountered this type. In their experience the heterostylous plants with the intermediate styles constituted well over 99 percent of the flowers observed. In view of the fact that this plant is otherwise well-adapted for insect pollination, it is interesting to ponder the paucity of heterostylous flowers which would promote cross-pollination.

The dimensions of the inflorescence bud, as well as the inflorescence, is extremely variable in nature. The length of the peduncles, bracts, subrachis, and rachis on the small plants are usually less than 40 percent of the length of comparable structures in the large plants. In view of the tremendous variation in vegetative parts and inflorescences, no average for the dimensions of the parts of water hyacinth plants in general can be postulated. Furthermore, the writers have felt that, with rare exceptions statistical data were valueless. They have, therefore, merely presented their averages of ten measurements for the parts of plants in given situations. The dimensions of the flowers constitute an exception to the general phenomenon of variability in the water hyacinth. Although the number of flowers vary greatly in small, medium, and large plants, the flower parts vary only slightly in size. Their experience showed that individual measurements of floral parts among any class of plants varied almost as widely as did those between floral parts of the three classes (small, medium, large).

Other workers should be cautioned about using detached inflorescences for experimentation since the parts are definitely smaller than in attached inflorescences when allowed to open with their bases in water. In general, the floral elements are about 30 percent smaller than similar components in the normal inflorescences. In addition to its smaller size, the floral axis often does not elongate sufficiently to carry all the flowers beyond the inflorescence bracts. Furthermore, floral opening is imperfect and the bending pattern subsequent to flowering is abnormal. In all studies entire plants with attached inflorescences should be utilized.

Anthokinetic Cycle

In nature inflorescence buds can be readily seen ten days before the flowers open. Ten plants, with very young inflorescence buds (average 25 mm.), were placed in tubs of water on a fire escape in midsummer and observed for floral development. The average height increment, preliminary to flowering, was about 15 mm. per day. Most of the elongation, however, occurred during the night of floral opening (about 250 mm.). The first bud to open (50 mm. long at start) flowered in 6 days and the last one (15 mm.) flowered in 11 days (average about 9 days). Since the buds were 25 mm. long at the start, it is necessary to add about 5 days to the period between the initiation of the inflorescence bud until opening occurs (total 14 days).

The anthokinetic cycle of water hyacinth consists of a flowering phase and a bending phase (Rao 1920). During the summer with average night and day temperatures of 75° F. and 90° F. respectively, the cycle is completed in about 48 hours. Inflorescence buds begin to issue from the inflorescence sheath about 5 P.M. (C. S. T.). By 9 P.M. about half of the lavender buds protrude through the sheath and all buds are exposed by 11 P.M. (Fig. 8). The individual flower buds now begin to bend downward toward the horizontal position and reach their final position (average 40°) by 4 A.M. Opening of the flowers is not initiated, however, until about 7 A.M. (well after dawn). At first the opening is very slow and gradual but this becomes more rapid as the halfway point is reached, and complete opening is usually accomplished by 8 A.M. (Fig. 8).

If a few, or even one of the apical flowers fail to open, the inflorescence remains in the vertical position until the following morning or until such later time as the apical flower buds open. If all the flowers of an inflorescence open, the peduncle remains erect until about 5 P.M. of the same day, at which time the bending phase is inaugurated. In the bending phase the flowering stalk begins to bend in three different places; at the rhizome crown (basal), about one inch below the two bracts of the inflorescence (capital), and in the rachis itself. By 11 P.M. the peduncle base has grown unequally to move the peduncle outward from the center of the plant, to an angle of about 70° and the upper portion of the peduncle has bent downward to an angle of 50°. This latter (capital) bending continues until the upper half of the flower cluster is nearly horizontal (0°) by 4 A.M. and completely inverted (−90°) by 7 A.M. (Fig. 8). Although the bending phase is often completed by 7 A.M., the writers' field observations indicate that most of the geniculate inflorescences do not attain the inverted position unti 5 P.M. (48 hours after the bud starts to open). The combination of the basal and capital bending is usually sufficient to thrust the entire flower cluster into the water unless some obstruction is encountered (Rao 1920). The sub-rachis, from bracts to the actual flower-bearing portion of the axis (rachis) bends very slightly but the rachis bends gradually upward throughout its length in such a way that the inflorescence tip is maintained in a nearly vertical position (Fig. 8).

Although the normal flowering phase consumes only one night for its completion in midseason, it requires a longer period with lower temperatures. Even in shade the initial opening is usually delayed a full hour in the morning. On cold days (night, 55° F., day 65° F.) opening was delayed 6 hours. Field evidence indicates that average daily temperatures much lower than 60° F. may delay flowering for several days. Support is given this conclusion from laboratory experiments. Inflorescence buds about to open were placed in a refrigerator at various temperatures for six-day periods with the following times required for complete opening: 50° F., five days; 65° F., four days; 70° F., two days; and

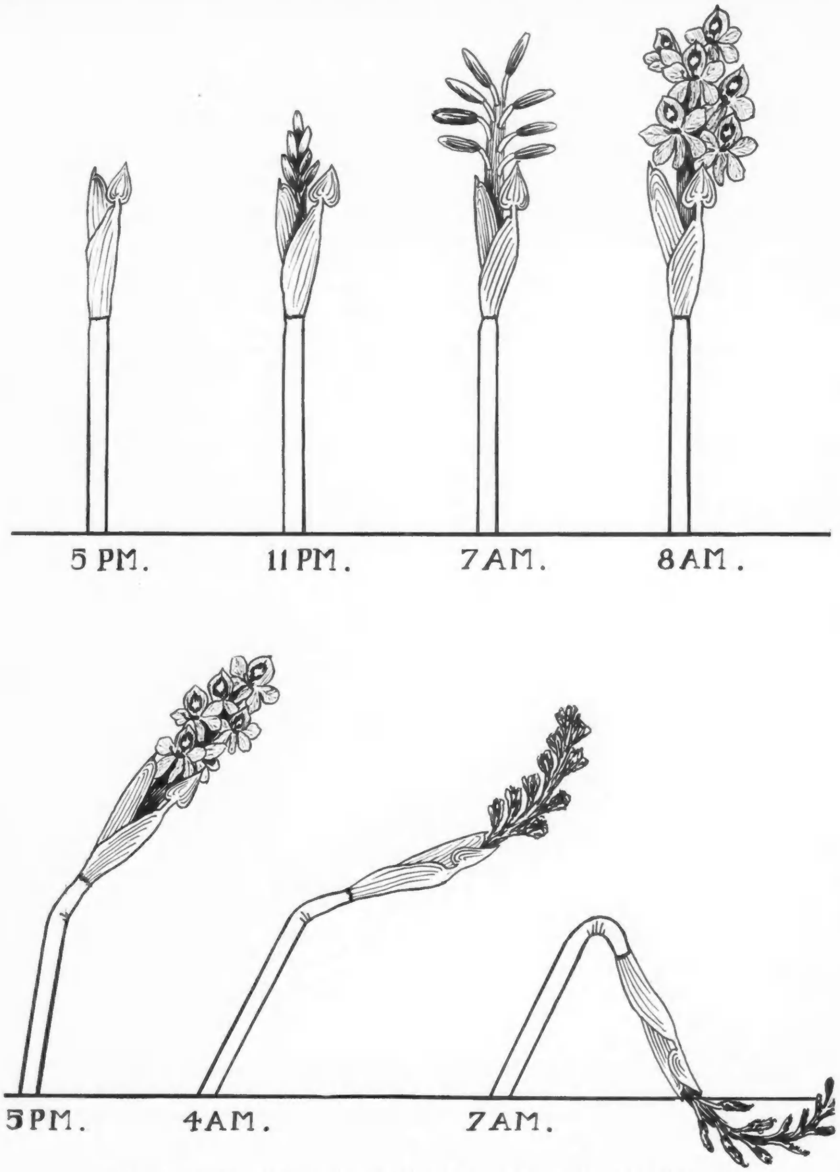

FIG. 8. Anthokinetic cycle, including flowering and bending phases.

75° F., about 16 hours, slightly longer than controls at 85° F. Temperature has a similar effect on the bending of the peduncle and rachis subsequent to flowering. In warm weather the flower cluster is directed downward into the water 23 to 33 hours after floral opening unless some obstruction is encountered. In relatively cold weather, however (night, 50°; day, 65°) bending was delayed one day, and in still colder weather, it was delayed for four days.

The day after flowering is completed the withered flowers are thrust toward the water surface by the geniculation of the peduncle. Whether the developing ovaries ever reach the water, maturation of the capsules continues. In general, a period of 20 (16 to 23) days is necessary for the production of ripe capsules. With self-pollination of tubbed plants fruit production occurred in 16 to 19 days whereas the formation of ripe capsules required 18 to 23 days on tagged plants under field conditions. Since flowering is inaugurated about April 1, the first capsules are matured about May 1. Ripe fruits may be collected until freezing weather terminates anthesis in late autumn (November or early December). As soon as, or perhaps somewhat before, the capsules

are mature the thin-walled pericarp dehisces. Since the capsule is enclosed in a hypanthium, this structure still invests the split capsule. Shortly after ripening, however, the hypanthium also splits and the fruit, with its exposed seeds, is cast off onto the mat or into the water. If they reach the water, they promptly sink to the bottom where they remain in a viable condition for several years.

Early in our studies it was observed that inflorescence buds which were exposed to artificial light during a portion or all of the night exhibited incomplete and delayed opening of the individual floral buds. Furthermore, difficulty was experienced in photographing floral opening because the exposure of the inflorescence bud to recurrent periods of relatively high light intensity caused abnormal and delayed opening of the flowers. In order to determine whether the time of exposure was responsible for the abnormalities observed, inflorescence buds in a similar stage of development were subjected to two-hour light periods at intervals throughout one night. Six batteries of three plants each were placed in containers in a dark chamber at approximately 6 P.M. At 6 P.M. and at intervals of 2 hours thereafter one battery of three plants each was removed from the dark chamber, exposed to a light of 10 foot candles for 2 hours and then placed back in the dark chamber for the remainder of the night.

When the inflorescence buds were brought out into the light earlier than midnight, the flower buds failed to open on time (8 A.M.). In the plants exposed at midnight, flowering was nearly normal, although complete opening was not attained until 9 A.M. (Table 12). When exposed to light at times later than midnight, the inauguration of floral opening was accelerated (Table 12). When exposed to light at 2 A.M., a greater degree of opening was accomplished by 4 A.M. than occurs in nature by 7 A.M. When exposed at 4 A.M., the perianth started to unfold within a half hour, the flowers had accomplished 70 percent of full opening by 6 A.M. and were fully opened by 7 A.M., a full hour ahead of schedule.

These data indicate that the light stimulus may either decelerate or accelerate anthesis in the water hyacinth. When applied at dusk or the early part of the night, anthesis is decelerated. Apparently darkness during this period is a necessary prerequisite to normal flowering and exposure to light interferes with the hormonal balance of the plant sufficiently to cause abnormalities in flowering. Since acceleration is accomplished by light exposure after midnight it is assumed that the early dark period has conditioned the plant in such a way that acceleration of anthesis by light is the inevitable sequel.

TABLE 12. Effect of time of exposure (2 hours each) to artificial light on the flowering of water hyacinth.

Time exposed	Percent of Full Floral Opening							
	8 P.M.	10 P.M.	12 Mt.	2 A.M.	4 A.M.	6 A.M.	8 A.M.	10 A.M.
6 P.M.	0	0	0	0	0	0	5	95
8 P.M.	......	0	0	0	0	5	10	98
10 P.M.	......	......	0	0	5	15	60	100
12 Mt.	......	......	......	0	20	40	90	100
2 A.M.	......	......	......	......	40	90	100	100
4 A.M.	......	......	......	......	......	70	100	100

The effect of the quality of the light on flowering was also studied. Two phototropic cabinets were constructed, consisting of three individual chambers 18 inches to a side, each of which was provided with a 3-inch opening. The cabinets were so constructed that free circulation of air was permitted without any mixing of light waves. One electric, 100 watt lamp, at a distance of six inches, was placed in front of each opening and light quality was procured by the use of red, yellow, green, blue and violet standard Eastman filters. Fifteen plants, whose flowers were certain to open the night of the experiment, were divided into five batteries of three each and placed in the phototropic chambers at 6 P.M. and subjected to continuous illumination until 10 A.M. the next day.

It will be recalled that, under natural conditions, the individual flower buds begin to push through the inflorescence bracts about 5 P.M., that they complete this operation by 11 P.M., reach the nearly horizontal position by 4 A.M. and accomplish opening by 8 A.M. In the case of all plants except those illuminated by blue light, the individual flower buds did not reach the final position (35°) until 6 A.M. The buds in the light under the blue filter reached the normal condition on schedule (11 P.M.) but continued to bend downward to a position only 5° above the horizontal by 6 A.M.

The actual opening of flowers proved most interesting. At either end of the spectrum (under red and violet filters) flowering was considerably delayed, and was incomplete at 10 A.M., two hours after the controls were fully open (Table 13). Floral opening under the green filter was very gradual and considerably ahead of the controls. Of greatest interest was the flowering of the plants under the blue filter (Table 13). Although the individual flower buds reached the normal position on schedule, no sign of opening had occurred by 5 A.M. In the course of an hour, however, nearly full opening had

TABLE 13. Relation of light quality to flowering of water hyacinth. Exposure period from 8 P.M. to 10 A.M.

	Time of observation				
	2 A.M.	4 A.M.	6 A.M.	8 A.M.	10 A.M.
Filter	Percent of full floral opening				
Red	0	0	5	30	80
Yellow	0	5	10	50	90
Green	5	30	95	100	100
Blue	0	0	90	100	100
Violet	0	0	0	10	30

been accomplished (almost 2 hours ahead of schedule). The significance of these diverse results is not immediately clear. It is believed that the differences are not related to temperature since temperature variations were insignificant in the various chambers. Although the results have been duplicated it is felt that further experimentation is necessary, with filters of localized, known transmission and with light of carefully measured intensity before detailed conclusions can be drawn.

POLLINATION

The question of the method of pollination has intrigued research workers for years. Despite the excellent adaptations of the flowers for cross-pollination by insects, no pollinators have been observed by many workers. The authors did not observe any insect visitors for 6 months, but on October 4, 1945, the senior author observed two honeybees visiting the flowers. Since that time we have observed honeybees, bumblebees, and black, unidentified bees and sulfur butterflies visiting these attractive, lavender blossoms. Honeybees which were most numerous exhibit three types of behaviour; visiting distal anthers only, alighting with the anterior end among the proximal anthers and the abdomen on the stigma and visiting the proximal anthers after alighting on the banner petal. It is doubtful whether much pollination was effected by any of these insect visitors. It was observed that these insects rarely visited more than one flower per inflorescence. Upon examining the stigmas of visited flowers, we were able to observe only a few pollen grains on the stigmas of some of the flowers. Our experience, therefore, led us to conclude that the desultory methods employed by these insects could not account for the considerable number of capsules (900,000 per acre) that have been observed.

The possibility of self-pollination was, therefore, investigated. The flower itself is nearly horizontal (facing outward from the inflorescence axis) but the individual floral axis points upward somewhat. The andro-gynoecial column, although the parts are separate, form a unit with reference to their angular disposition (Fig. 7). The short stamens and the long stamens are disposed at an angle of 9° whereas the style is disposed at a slightly greater angle (12°) with (and above) the horizontal axis. In view of the fact that the andro-gynoecial column is almost horizontal, and the fact that the stigma is about halfway between the two sets of anthers it is evident that self-pollination is almost impossible in the fully opened flower.

That the flower was self-fertile was proven by the junior author who carried out hundreds of self-pollinations by hand and obtained ripe capsules in nearly every case. From these facts the writers could only conclude that self-pollination must be important in the water hyacinth. Therefore, they decided to examine stigmas for pollen in: unopened buds, fully open, slightly wilted and completely wilted flowers. Flowers of water hyacinth begin to close at 5 P.M., inflexing of the tips of the sepals and petals begins at about 9 P.M., and is completed at about midnight at which time a twisting or spiralling is initiated. Pollen was rarely encountered on the stigmas either in the unopened buds or in the open flowers in the laboratory. Some pollen was found on a few stigmas in the slightly wilted flowers (with inflexed perianth). Much pollen, on a considerable number of stigmas, was found in the completely wilted flowers (with spiralled perianth). From the above it is obvious that self-pollination due to inflexing, and especially due to spiralling, of the perianth is very common in the water hyacinth.

SEED GERMINATION

Where a mat of water hyacinth is well-developed there are abundant seeds both in the peaty turf of the mat and on the bottom underneath the mat. The writers have observed seedlings on exposed shorelines, on rotting logs, in natural water hyacinth mats, especially when invaded by cattail, and on decaying mats sprayed with formagenic herbicides. They have obtained abundant seedlings merely by inverting a number of plants on the mat and by removing living or dead plants from the mat. These platforms present such ideal conditions for seedling development that the writers utilized this method regularly for procuring seedlings. These observations indicate that drying out is unnecessary for germination (as claimed by Parija 1932, and others) but suggest that increased light intensity may be important.

The statement has often been made that reproduction in water hyacinth is mainly by seeds which germinate under water and rise to the surface subsequent to germination. But Robertson and Thein (1932) reported that "on no occasion were seedlings formed in permanent, standing water." The writers have never been able to find any submerged seeds which have germinated under natural conditions nor have they been able to germinate seeds under water in the laboratory. They found that seedlings already well established (30 days old) confined in floating wire baskets showed very poor development. When placed in small pools of water in an opening in a well-developed mat, presumably with low oxygen tension, none out of ten survived. Out of ten seedlings placed in a borrow pit for a month, four were healthy but showed poor color and little growth, four were sickly, and two were dead, undoubtedly due to heavy competition from *Azolla*, *Spirodela*, and *Lemna*. Whenever older plantlets (40-90 days) were removed from the mat and placed in water they grew at a very rapid rate (at least double that of similar plants on the mat). It appears, therefore, that young seedlings (3-40 days) do best on a solid substratum whereas plantlets (40-90 days old) develop best on a water surface.

In general, the first seedlings can be seen with a hand lens in 3 days after the preparation of the "seed bed." The first structure to emerge is the cylindroidal cotyledon, followed shortly by the roots and the leaves (Fig. 9B). In 10 days, the seedlings

will have produced 2 or 3 ligulate leaves which make them readily visible. In 20 days, all the cotyledons will have disappeared, and the plantlet will have produced 4 to 6 ligulate leaves about 15 mm. in length (Table 14). In 30 days the seedlings will have produced 7 or 8 ligulate leaves and 1 to 3 spatulate leaves with incipient floats (Fig. 9D). In another ten days (40 days from germination) float leaves will have been formed and the seedlings are readily recognized as water hyacinth plantlets. Rob-

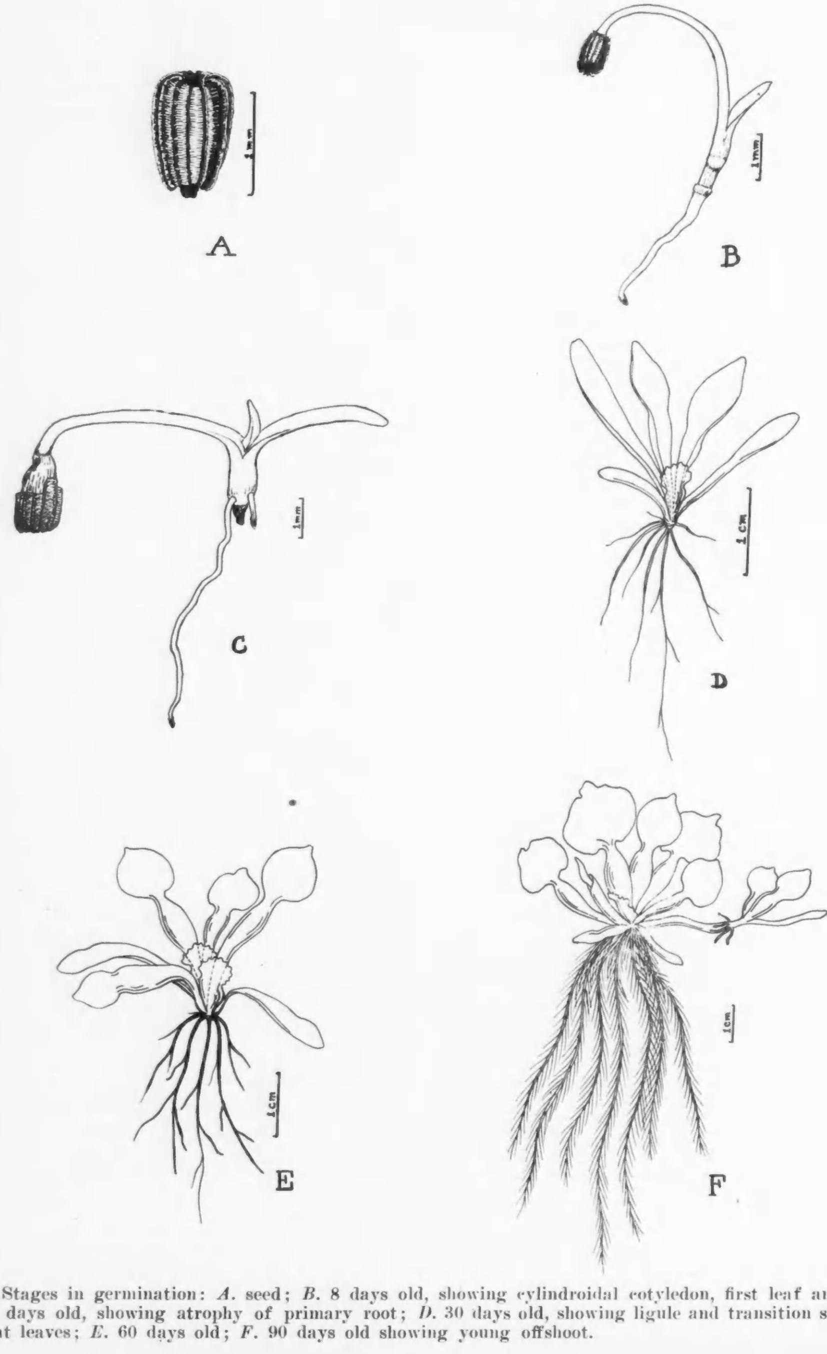

FIG. 9. Stages in germination: *A.* seed; *B.* 8 days old, showing cylindroidal cotyledon, first leaf and primary root; *C.* 10 days old, showing atrophy of primary root; *D.* 30 days old, showing ligule and transition stages from strap to float leaves; *E.* 60 days old; *F.* 90 days old showing young offshoot.

ertson and Thein (1932) reported that seedlings added one new leaf about every three days. As development progresses the lower leaves continue to die off with the result that the number of leaves remains constant. In 60 days a majority of the leaves will be of the float type and new, but tiny offshoots may be produced (Fig. 9E). From this time onward, the plantlets produce stolons, rhizomes, leaves, and eventually flowers and fruits.

In none of the seedlings produced in our plots in 1946 (June 22-Sept. 23) did any flowering take place during the 1946 growing season. By May 10, 1947, the seedlings produced on June 22, 1946, possessed leaves 3 inches long and had initiated flowering. By May 25, 1947, seedlings that started germination on June 22, July 16, July 25, August 3, and August 21, in the previous growing season had produced some flowers. Only the seedlings of September 23, 1946, had failed to produce flowers by this date. From the above results, however, it is apparent that the life cycle (seed to seed) is a very slow process in nature since it was not accomplished by any of our plants during the first season (5 months, from June 22 to November 22).

TABLE 14. Rate of seedling development on cleared mat.

	Number of days from beginning of germination.						
	3	5	10	20	30	60	90
Cotyledons							
Color	Colorless	Green	Green				
Length, mm.	2	3	7				
Ligulate Leaves							
Percent of total	..	100	100	100	80	40	5
Length, mm.	..	1	9	15	18	18	17
Float Leaves							
Percent of total	..	..	..	..	20	60	95
Length, mm.	..	..	..	..	14	30	40

Although seeds are abundant in the raw peat of the mat, seedlings have been observed only in open spots caused by the death of some of the water hyacinth plants. As has been indicated, germination can be induced on the peaty turf merely by removing living plants from the mat. In an attempt to ascertain whether sunlight was important, the writers placed portions of the raw peat in large fingerbowls in full sunlight, diffuse light, and darkness. Seedlings were obtained only in full sunlight. The experiment was repeated under very similar conditions of temperature and humidity and again the same result was obtained. These observations suggested that sunlight was necessary for the germination of these seeds under natural conditions.

Further experiments, however, proved the fallacy of this belief. In an attempt to determine the percentage of germination of seeds collected from a water hyacinth mat on January 15, 1947, very different results were obtained. Four sets of 10 seeds each were placed on wet sawdust and placed in full sunlight and indoors by an open window but no germination occurred. Eight sets of 10 seeds each were placed on wick germinators, with two sets each being disposed as follows: full sunlight, window light, diffuse light, and darkness. Only 1 of the 80 seeds germinated. It was found also that none of the seeds, which failed to germinate, had increased in size. Parija (1934) pointed out that the failure to swell was due to mechanical resistance of the seed coat. The writers also resorted to heat treatment in an incubator for periods of 1, 2, 4, 8, and 16 days but none of these seeds germinated. They then resorted to scarification. Six sets each of 10 scarified seeds were placed in petri dish germinators and two sets each were disposed in window light, diffuse light and in darkness. In 5 days the following percentage germination was obtained: window light, 35; diffuse light, 29; and darkness, 40. These experiments demonstrate that scarified seeds germinate readily and suggest that scarification, by either physical, chemical or biotic factors is a prerequisite for the germination of the water hyacinth seeds. It also demonstrates that light *per se* is not a prerequisite for seed germination. It is probable that the removal of the water hyacinth canopy changes other conditions in the mat, such as temperature, which then permit scarified seeds to germinate.

CONTROL METHODS

The water hyacinth was officially recognized as a serious aquatic pest when Congress passed an act on June 4, 1897, authorizing the Secretary of War to investigate the extent of obstruction to navigation in the waters of Louisiana and Florida. From 1897 to the present the Corps of Engineers has attempted, with moderate success, to keep the waterways in infested areas open to navigation. In this program they have employed various mechanical devices such as the bank-depositing machine, the crusher, and the saw-boat. In addition, they utilized sodium arsenite in an extensive spray program but abandoned this chemical because of danger of poisoning to livestock and man. However, it should be pointed out that the objective, in all cases, was merely the clearing of channels for navigation, and not the control or eradication of the pest.

In the control of water hyacinth there are three types possible: mechanical, chemical, and biological. Up to the present no biological means of control have been attempted but both mechanical and chemical methods have been used with some success. Bank deposition has proven entirely too costly; crushing has been fairly effective but again too expensive; but sawing in place, with rotating circular saws about one inch apart, has been used rather extensively during the past eight years. The method is fairly effective except that considerable resprouting of the segemented material occurs. If more efficient segmentation of the mat can be accomplished, this method should become reasonably practical.

All chemical treatments to date have run into the difficulty that the sprayed and killed plants did not sink. This is not surprising in view of the fact that a chopped-up mat does not sink completely for at least six weeks. When sprayed with sodium arsenite, the mat remains afloat for a similar period and when sprayed with the formagenic phytocides containing 2,4-dichlorophenoxyacetic acid (2,4-D), they continue to float for an even longer period. If the mat is well developed, the germination of seeds of the hyacinth and other plants continues on mats which have been sprayed at monthly intervals for four months. It is true that sprayed mats which are subjected to the action of currents, wind, waves, and power-boats do sink somewhat more rapidly but this help does not eliminate the problem completely.

Airplane spraying and dusting of water hyacinth using compounds containing 2,4-D have proven fairly effective and inexpensive. Dusting has one disadvantage in that the dust must be applied when the vegetation is wet with dew or rain. Excellent results have been obtained in the open but the greatest decimation of water hyacinth (over 99.9 percent with one application) was obtained under a stand of bald cypress with moderate crown cover with the butyl ester of 2,4-D in kerosene. That the destruction of the hyacinth by this formulation is greater in the shade has been observed elsewhere in the field and proven in the laboratory. In the past it has been the practice to use dilute sprays of 2,4-D but at present the oil-soluble esters have been used in total amounts as low as one quart per acre with satisfactory kill of this aquatic pest. This means that the application of spray materials by air is a practical operation.

The airplane application of both dusts and sprays was attended by certain difficulties in the summer of 1947. In North Louisiana, 2,4-D dust caused formagenic effects on cotton and other plants 1½ miles from the flight line. A similar circumstance, but using a spray, was experienced in North Alabama. In both cases young cotton plants were apparently seriously injured but recovered sufficiently to produce an excellent crop. At a later date in 1947, cotton in full flower was inadvertently dusted with 2,4-D with disastrous results. From these, and other experiences, it is obvious that great care must be exercised in applying dusts and sprays by airplane. At present, experiments are under way to produce dusts of larger particle size and it is planned to initiate experiments in 1948 to modify spraying techniques to prevent drift and possible crop damage.

The future of water hyacinth control is still uncertain due to difficulties in obtaining adequate appropriations and the proper cooperation between private, state, and federal agencies. Several writers feel that this pest could be eliminated readily if some commercial use could be found. The authors, however, agree with Buckman (1920) who concluded that "no commercial utilization of the hyacinth on any scale likely to be a factor in a campaign for eradication or control is to be expected." Undoubtedly we now have the technical knowledge to control or even to eliminate the water hyacinth from the country. If this pest causes $5,000,000 damage annually, then it is obvious that at least that much money can be afforded per annum for its control. If this amount of money were available, it would be possible to reduce the water hyacinth to the vanishing point in five years and eventually to eliminate it from the United States of America.

SUMMARY

The water hyacinth is a perennial, mat-forming, floating aquatic of wide distribution in tropical, subtropical, and warm temperate regions throughout the world. It has been reported from all the southeastern coastal states as well as from California. Damage caused by this pest has been variously estimated to be from one million to fifteen million dollars per annum in Louisiana alone, the greatest damage being caused by obstructing navigation and by destroying wildlife resources.

The mature plant consists of roots, rhizomes, stolons, leaves, inflorescences, and fruit clusters. The roots are white in rooted plants but tinged with purple in floating plants. The rhizome produces all roots and leaves, as well as the reproductive structures: offshoots and inflorescences. Its reproductive tip (average 1 in. long) rests about 1.5 (0.5-3) inches below the water surface. The purplish stolons (2-18 in. long) are nearly erect in dense stands but become horizontal in open colonies. In open conditions, the leaf consists of a membraneous ligule, a subfloat, a float (swollen mid-portion of petiole), an isthmus, and a blade which is merely a flattened portion of the petiole. The stomata are very large (12 x 27 microns), vary from 0-120 per square millimeter from the base to the tip of the leaf, and are very sensitive to habitat conditions.

In the New Orleans area, growth of the water hyacinth is continuous from March 15 to November 15 and discontinuous during the winter. Obvious greening of the mat is evident by April 1 and flowering is inaugurated about April 15. Maximum anthesis occurs about June 1 and a second but lower maximum prevails about September 15.

A predominant role in succession is played by the water hyacinth by providing a floating platform for the ecesis of terrestrial, wetland and aquatic species. These species form a floating marsh (flotant), which continues to increase in thickness (build downward) until its base may come to rest on the bottom. A mat of water hyacinth plants of medium size (800,000 per acre) was found to have a loading capacity of nine pounds per square foot. Although all parts of the plant floated, the low specific gravity of the floats (0.136) is responsible for the considerable buoyancy of the mat. The total material (wet weight) in an eight-year old mat varies from 123 tons per acre in winter to 184 tons per acre in summer.

The water hyacinth occurs in all natural and artificial (except brackish and saline) waters in the

Gulf Coastal states. It may eize on land but is usually killed by frost during the dormant period. Variation in size is tremendous under natural conditions, rooted plants on gravelly shorelines having leaves only 3 inches long and as few as 2 flowers per inflorescence whereas plants in well-aerated canals may have leaves 50 inches long and as many as 38 flowers per inflorescence.

Since leaves do not produce floats in crowded conditions (normal mat), in shade, or on land, very few leaves in nature possess floats. Floatless leaves are formed when the average light intensity drops below 500 foot-candles and death supervenes when the intensity remains continuously below 130 foot-candles.

Water hyacinth cannot tolerate water temperatures higher than 34° C. (93.2° F.) for extended periods. Leaves are killed by freezing temperatures but entire plants are not destroyed until the rhizome tip (1.5 inches below surface) is frozen.

The water content of this species averages about 95 percent (89.3 in leaf blades to 96.7 in stolons). Total transpiration from water hyacinth averages 3 (2.6 to 6.6) times that of evaporation from a free water surface. Plants, deposited on an open lawn, survive for 6 days in sunny weather and up to 12 days in cloudy weather. When rooted plants are reflooded during active growth they abscise just below the lowest living leaves and float to the surface, but when reflooded near the end of the growing season they remain on the bottom and perish. When plants are forcefully submerged, they exhibit increasing paleness, epinasty, and exfoliation of parts but survive for a long time (up to 39 days).

When this species is subjected to brackish water, epinasty, and usually chlorosis, were constant forerunners of necrosis and death. The evidence does not indicate that this fresh water plant is adjusting itself to saline waters.

Vegetative propagation is more important than sexual reproduction in colonization by the water hyacinth. Under good growing conditions, a mat migrates at the rate of 2 feet per month and the plants double their numbers every 2 weeks by means of offshoots. At this rate 10 plants would produce 655,360 plants (a solid acre) in one growing season (Mar. 15-Nov. 15).

Although the flower appears to be excellently adapted for entomophily, pollination by insects rarely occurs because only one type of heterostylous flowers is abundant in the New Orleans area. Self-pollination during wilting is a common phenomenon, however. The anthokinetic cycle (48 hours consists of a flowering phase: 5 P.M. to 8 A.M. and a bending phase: 5 P.M. (2nd day) to 5 P.M. (3rd day). Low temperatures increase the time required for completion of both phases. Supplementary white light during the flowering phase decelerates floral opening when applied before midnight but accelerates anthesis when administered after midnight. About 18 days after pollination the ripe seeds are shed either on the mat or on the bottom where they remain in a viable condition for several years.

Seeds germinate only when exposed to the air, seedlings being present on exposed shorelines, rotting logs, dead spots in mats, and on mats sprayed by herbicides. During germination the following sequence occurs: 3 days, cylindroidal cotyledon only; 10 days, roots, cotyledons, ligulate leaves; 30 days, roots, ligulate leaves, a few incipient float leaves; 60 days, roots, float leaves, offshoots. Seedlings with ligulate leaves do not survive in open water but float-leaved seedlings thrive better in open water than on the mat.

Of the mechanical control methods, bank deposition has proven very costly, crushing has been fairly effective but too expensive, and the saw-boat has proven relatively ineffective because the segmented material remains afloat for long periods (6 weeks or more) and resprouts considerably. Of the chemical methods, spraying with sodium arsenite has been abandoned because of the hazard to livestock and man, but dusting and spraying with compounds containing 2,4-dichlorophenoxyacetic acid, particularly by airplane, have proven fairly effective and relatively inexpensive. It is felt that at present the technical knowledge is available to control or even to eliminate the water hyacinth from the United States of America.

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BIOTIC COMMUNITIES OF THE WASATCH CHAPARRAL, UTAH

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BIOTIC COMMUNITIES OF THE WASATCH CHAPARRAL, UTAH

INTRODUCTION

To the observant traveler who approaches the Wasatch Mountains from the broad desert valleys of western Utah several features are strikingly apparent. The abruptness with which the mountains rise from the valley floor; the clear shorelines and deltas of the ancient Lake Bonneville; the deep erosional and glaciated canyons; and the summer verdure of the chaparral that covers the lower portions of the mountain slopes—all are characteristic of this mountain range rising out of a land predominantly desert.

The vegetational aspect of the Wasatch front presents a strikingly variable appearance throughout the seasons. In late spring, it is fresh green with the newly formed leaves of the deciduous chaparral and June grass. By early summer the greenness of the chaparral has deepened and the grassy areas between the shrubs have ripened and turned brown. In late August or early September patches of crimson appear in the higher elevations as the maple begins to assume its autumnal colors; and then, as the season advances, the multi-colored reds, yellows, and browns gradually appear changing the entire aspect of the vegetation. By late October or early November, the pigmented leaves have begun to fall and the dull gray aspect of winter predominates until the middle or latter part of the following May.

The biotic condition which prevailed in this community previous to the settlement of valleys adjacent to the Wasatch by the Mormon pioneers, is largely a matter for conjecture, although certain historical aspects of the community will be discussed later in the paper. However, the close proximity of this area to the farming lands of the valleys naturally led to its early and too often abusive use by the settlers from the very first, with the result that it was very soon exploited to the full and the biotic changes wrought upon it were undoubtedly of great significance.

On account of the steepness of the terrain and the difficulties of irrigation the area occupied by the chaparral has never been extensively cultivated. Its principal use has been as a pasture land with the result that the greater part of it has become overgrazed to the point where many of the perennial forbs and grasses have been largely eliminated and only the annual weeds and grasses and the more unpalatable shrubs remain. Certain portions of the Wasatch chaparral are important wintering grounds for deer, and the range has undergone considerable modification on that account. Furthermore, the close proximity of this community to the cities and villages located along the base of the Wasatch has made it easily accessible to hunters and hikers who have undoubtedly done much to upset the natural conditions of the area.

The net result of all these human activities has been to modify the natural biotic condition of the Wasatch chaparral to a point impossible to ascertain. The present biotic analysis, therefore, is based upon conditions as they obtain today, with little opportunity, unfortunately, to understand the circumstances that prevailed previous to the advent of the white man.

The writer desires to express appreciation to the following individuals who have contributed in one way or another to the progress of this work. Dr. F. S. Harris, formerly president of Brigham Young University, has made available some funds from the research money of the university for equipment and travel expenses. Dr. V. E. Shelford of the University of Illinois gave much helpful advice and encouragement during the early part of the study and visited some of the field stations. Several individuals have contributed materially by identifying material in all of the animal and plant groups. For this kindly service the writer expresses appreciation to the following: Dr. Bertrand F. Harrison and Mrs. Desma H. Galway, plants; Dr. Ralph V. Chamberlin, spiders, chilopods, and diplopods; Dr. C. W. F. Muesebeck and a number of his co-workers at the Bureau of Entomology and Plant Quarantine, mites and several orders of insects; Dr. Vasco M. Tanner, beetles; Dr. George F. Knowlton, aphids; Dr. D. Elmo Hardy, Diptera; and Dr. H. M. Harris, Hemiptera. Mr. Wilmer Tanner also contributed some valuable information from his notes regarding the distribution of some of the reptiles.

FIELD WORK AND METHODS

Field work in the Wasatch chaparral was begun by the writer as early as 1931 and has continued somewhat intermittently to the present time. The earlier work consisted mainly of general observations and collections, particularly of the birds. From 1938 to 1941 quantitative as well as qualitative ecological work was undertaken in the upper part of the chaparral, particularly on the east slope of Mt. Timpanogos, and a brief summary of this work was later published (1942). Field work was resumed in 1944 and 1945 with concentrated efforts on the lower part of the chaparral on Y Mountain directly east of Provo. During these two seasons quantitative and qualitative work was done at intervals, usually of one or two weeks, throughout the summer months. Pressure of other work prevented any other than general observations throughout the winters.

Ecological methods employed in the study were essentially the same as those used in previous studies and described in some detail in a previous work (1945). These methods will not be repeated here

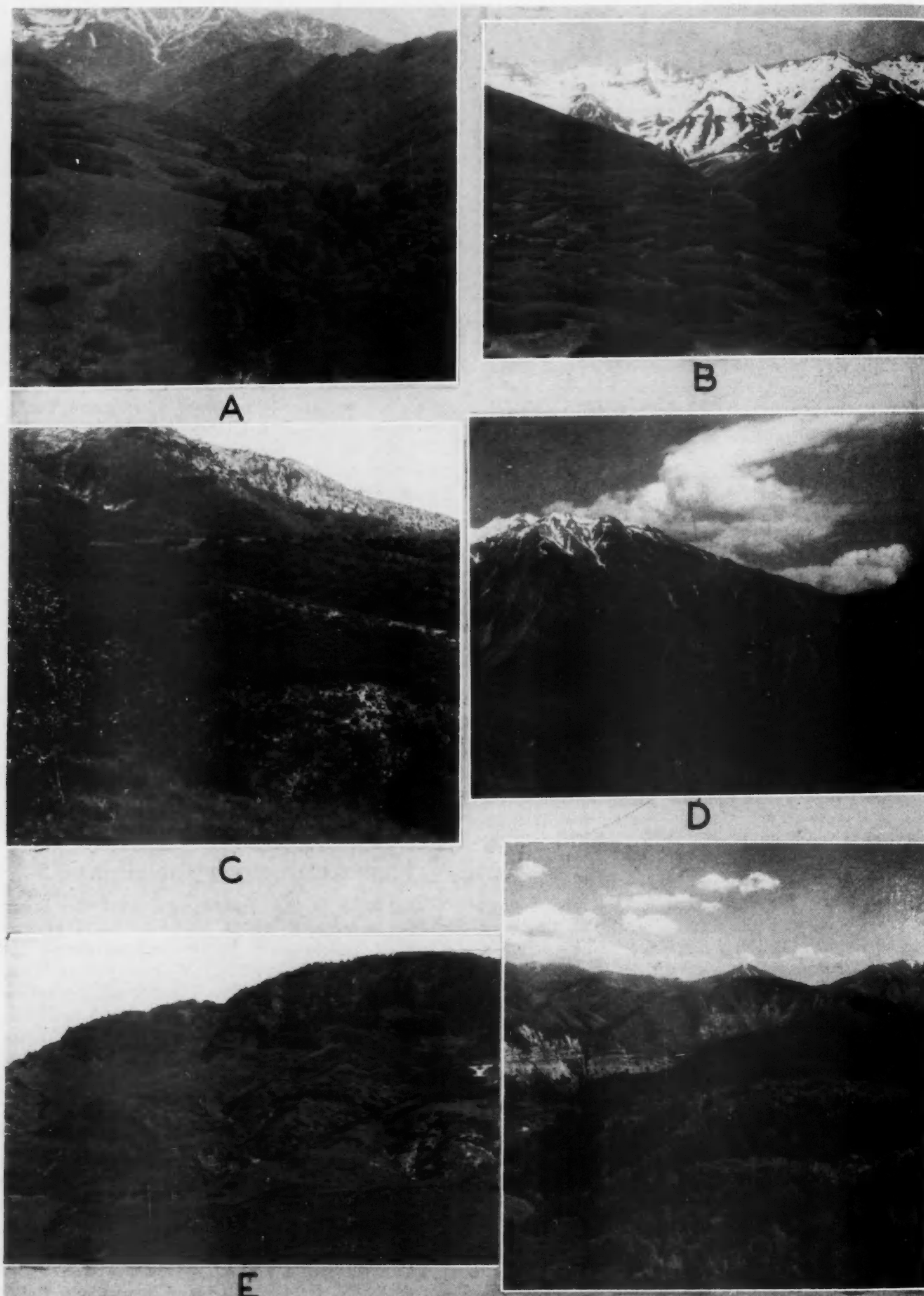

FIG. 1. Several views of Wasatch chaparral. *A.* Portion of Dry Canyon, west slope of Mt. Timpanogos, showing scattered clumps of oak chaparral on southfacing slope and dense chaparral in canyon bottom and northfacing slope. *B.* Similar to A but showing snow-covered Mt. Timpanogos in background. *C.* Portion of chaparral on west slope of Mt. Timpanogos. *D.* Pole Canyon with chaparral slopes. *E.* Y Mountain east of Provo, Utah, showing location of Station 7. *F.* North Fork of Provo Canyon showing general location of Station 2.

except to mention certain departures from earlier methods in the course of this paper.

PHYSICAL FEATURES

The physical features which are of prime importance in any consideration of the chaparral biotic communities are associated with the geological origin of the Wasatch Mountains and with the influences of water erosion, glaciation, and lake deposition and erosions that attended them at intervals since they were first thrust up from the original peneplain. Detailed discussions of the geologic origin of the Wasatch Range may be found in the works of King (1878), Gilbert (1928), and Schneider (1930) and the writer has summarized their findings in a previous paper (1945). Atwood (1909) has described the glaciation in the Wasatch, and Gilbert (1890) has described Lake Bonneville in considerable detail.

The Wasatch Range occupies a comparatively narrow strip roughly between the 39th and 42nd degrees of latitude and between the 111th and 112th degrees longitude. A small spur, known as the Bear River Range, extends even into southeastern Idaho, but the chaparral herein discussed does not occur on that portion of the range.

The Wasatch Mountains form the east rim of the Great Basin. They rise abruptly from the floor of that basin to a jagged crest with some peaks reaching an elevation of more than 12,000 feet, and then slope away more gently toward the east. The western front is cut by many erosional canyons of varying depths and in certain places, notably Little Cottonwood Canyon, the Pleistocene glaciers descended even to the valley floor, leaving their typical U-shaped canyons and well defined moraines.

The chaparral of the western Wasatch front occurs in general above the highest shoreline of the old Lake Bonneville at an elevation of about 5,100 feet and extends upward to about 7,500 feet, where it meets the montane forests. However, the extent of the community is greatly modified by exposure and the definition of its limits by altitude alone is quite impossible.

In spite of the fact that climate must be recognized as a most vital physical factor in the determination of a biotic community, we are still largely in the dark as to the precise effect of the several climatic factors upon the organisms that inhabit the communities. This type of information can be obtained only by subjecting every organism to carefuly controlled field or laboratory procedures. While considerable work in this direction has already been done by ecologists, we are as yet able to draw only broad and general conclusions as to the exact influence of the climatic factors, especially in regard to the major biotic communities.

The influence of climate in the establishment and maintenance of plant formations and associations has long been understood by plant ecologists; and this concept has been championed in this country especially by Clements (1938: 478). On this basis climax formations are controlled by the sum total of climatic conditions within their habitats and serve as a biological expression of these conditions. The direct effect of climate upon animals is more obscure, mainly because these organisms are better able to adjust themselves to a variety of climatic conditions through locomotion, estivation, hibernation, dormancy, migration and through a greater ability to regulate body temperature and water.

Insofar as the present study is concerned the role of the climatic conditions in the chaparral are practically unknown; and indeed, there is little information regarding the climatic features that prevail within this community. The reader should understand, therefore, that the greater part of the climatic features here discussed are only an indication of the prevailing climatic characteristics as they compare with bordering communities and serve as the controlling factors of the climax.

In an ecological study of a single community, the microclimates are equally as important as the macroclimate, especially with reference to the distributional nitches of the animals. Whereas the overall or macroclimate determines the state of the climax; the microclimates undoubtedly have much to do with the distribution and habits of the animal constituents within the several nitches.

The macroclimatic data are generally of the type supplied by the Weather Bureau and include maximum, minimum, and mean temperatures, percent of relative humidity and precipitation. Such information serves well to indicate the climatic conditions which determine the climax vegetation. For the Wasatch chaparral, the most extensive data available are those of Sampson (1918) and Price & Evans (1937) taken at the Great Basin experiment station, Sanpete County at an elevation of 7,655 feet. General climatic data compiled from their reports and compared with data for Manti, Utah located in former grassland are summarized as follows:

PRECIPITATION (1919-1930)

	Annual Precipitation
Montane Forest (elevation 8,700 ft).	29.31
Chaparral (elevation 7,655 ft.)	17.64
Pinon-Juniper, Manti (elevation 5,575 ft.)	12.40

TEMPERATURE, °F.

	Mean Annual	*Extreme Max.*	*Extreme Min.*
Montane Forest	38.0	88	—26
Chaparral	42.6	97	—30
Manti	46.9	101	—30

The trend of precipitation throughout the seasons over a twenty-year period, according to data furnished by Price & Evans (1937) shows March the highest with over 4 inches and June the lowest with less than 1 inch. The great bulk of the precipitation falls between December and May. The trend of monthly mean temperatures shows a very regular curve that begins with January, which is the coldest month (monthly mean 22° F.) and rising evenly to July, which is the warmest month (monthly mean 65° F.). There is then a gradual decline to December which is about as cold as January.

The data of Price & Evans place the general climatic conditions of the chaparral as intermediate in all respects between the montane forest and the pinon-juniper woodland which has a climate much like the former grassland. However, certain factors not clearly indicated by ordinary climatic data are of great importance in ecological considerations and it becomes highly desirable for a more thorough understanding of these factors.

It should be borne in mind that the greater portion of the Wasatch chaparral occupies either south or west facing slopes which are usually steep. As a result, these slopes are exposed to direct sunshine for long periods of the day and the earth is able to absorb large quantities of heat, which is radiated at night. From fragmentary data gathered by the writer there is an indication that the minimum temperatures are higher in the chaparral, at least in summer, than they are in the valley grassland. Minimum temperature figures either taken daily or over various periods of time in three different stations in the chaparral, indicate that more often than not the temperatures are higher in the chaparral than they are in the valley at Provo. The writer's thermometers were not standardized but by comparison with other instruments are believed to be quite accurate. These data are indicated in Tables 1 and 2.

Maximum temperatures are not presented in the tables because the thermometer was not housed in complete shade and it is felt that the figures are not comparable. However, it is quite evident from the data at hand that maximum temperatures are on the average about ten degrees lower at Station 2 in the upper part of the chaparral than they are at the Provo level, but are about the same in the lower chaparral at Station 7 as they are at Provo.

TABLE 1. Comparison of minimum temperatures at Provo, Utah and lower Wasatch Chaparral (Station 7) taken during periods throughout the summer months. Degrees F.

	Chaparral (el. 5,200 ft.)	Provo (el. 4,500)
May 6 to 12, 1944	42	34
May 13 to 18, 1944	36	37
May 19 to 26, 1944	36	34
May 27 to June 6, 1944	36	37
June 7 to 20, 1944	40	36
June 21 to July 3, 1944	40	39
July 4 to 14, 1944	56	42
July 15 to 24, 1944	56	47
July 25, 1944	63	48
July 26, 1944	62	44
July 27, 1944	62	41
July 28 to 29, 1944	64	41
July 30 to August 9, 1944	56	40
August 10 to September 7, 1944	49	38
September 8 to 14, 1944	57	39
September 15 to 17, 1944	42	39
September 18 to 19, 1944	46	40
May 11 to 22, 1945	32	33
May 23 to June 8, 1945	32	32
June 9 to 12, 1945	40	37
June 13 to 14, 1945	36	37
June 15 to 26, 1945	30	32
June 27 to July 12, 1945	42	34
July 13 to 20, 1945	57	43
July 21 to August 10, 1945	50	46
Average of all records	46−	38−

TABLE 2. Comparison of minimum temperatures at Provo, Utah and upper Wasatch Chaparral on days taken at random during June and July. Degrees F.

	Chaparral (el. 6,800 ft.)	Provo (el. 4,500)
June 12, 1940	47	45
June 13, 1940	52	44
June 14, 1940	54	50
July 3, 1940	53	50
July 4, 1940	52	54
July 5, 1940	56	58
July 6, 1940	54	54
July 27, 1940	56	65
July 28, 1940	54	60
July 29, 1940	58	56
July 30, 1940	53	54
June 1, 1941	33	42
June 2, 1941	36	40
June 3, 1941	44	44
June 4, 1941	40	43
June 5, 1941	39	49
Average of all records	48+	50+

The lowering of temperature with a rise in altitude has generally been assumed and of course prevails where great altitudinal changes are involved. However, this rule may not hold true insofar as the temperature of the chaparral versus the valley grassland is concerned. It may ultimately be shown that insofar as the total heat available to a living organism is concerned, the climate is actually warmer in the chaparral than it is in the valley. This is because of the factor of slope exposure which counterbalances the influence of altitude and tips the scale in the direction of a warmer climate. At the upper limit of the chaparral, the influence of altitude overcomes the effect of slope exposure and a new type of community, the montane forest, prevails. If this theory is true, then the chaparral is limited both above and below by a colder climate—above by a lower maximum and below by a lower minimum.

The effect of slope exposure upon winter conditions in the chaparral is also evident to any observer who has watched the situation over a number of years. Most of the slopes occupied by the community are barren of snow throughout the greater part of the winter. Even heavy snows are melted from the exposure within a few hours or at most a few days after they fall, whereas they may form a nearly complete ground cover for weeks at a time in the valley and at higher elevations where temperatures are lower. Taking advantage of this exposure of winter feed, many thousands of seed eating birds winter within the chaparral and numerous small mammals are active even during the coldest portions of the winter.

Unfortunately there is very little information

available regarding the availability of water to the organisms of the chaparral. The amount of precipitation does not give much of a clew to the situation, since the problem of soil, water, relative humidity and evaporation so vital to plants are not indicated. Price & Evans (1937) show that there is on the average about five inches more precipitation annually in the chaparral than in the pinon-juniper. However, their station was at a rather high elevation and it seems doubtful if their figure would hold true for the chaparral community as a whole. Even if the total precipitation were greater, the rapid drainage and evaporation due to steep slopes probably makes even less water available to the plants than obtains in the communities of the level valley.

Evaporation data taken by the writer with standardized Livingston atmometers show a considerably higher evaporation rate in the chaparral at Station 7 than at Provo in the valley. Instruments placed in shade with moderate protection from wind about one foot from ground surface showed the following evaporation rates in August in clear weather:

	cc. per hour	*cc. per day*
Provo (el. 4,500 feet)	1.10	26.40
Y Mountain chaparral (el. 5,600 ft.)	2.34	56.16

Instruments placed about one foot from ground surface in open areas fully exposed to sun and wind on a west facing slope at 5,600 feet elevation showed an evaporation rate of 3.46 cc. per hour or 83.04 cc. per day. While these data are not extensive enough to be conclusive they indicate at least that the loss of water in the chaparral community is very rapid and presents a difficult problem of adjustment for both plants and animals.

Certain microclimatic features, particularly of the soil, will be considered in more detail under the discussion of the biotic matrix.

THE BIOTIC MATRIX

The complex of plant and invertebrate organisms which constitute the basic structure of the community may be conveniently considered as a biotic matrix. This arrangement is more of an organizational convenience than it is an ecological entity, but in general it consists of the more fixed constituents of the biotic community. It includes the living plant material and the invertebrate animals, either active or in some state of dormancy, which live in or on the plant material, or else are parasites upon other invertebrates within the matrix.

The larger animals, mainly vertebrate, move more or less widely through the community, are far less abundant than the organisms of the matrix, and may be only seasonally present as in the case of migrant birds and mammals. These larger organisms may be conveniently called permeant influents of major or minor importance depending upon the influence they exact upon the matrix. If their effect is sufficiently great, as in the case of overpopulation of deer to actually control the matrix, they may be called dominants. However, constituents of the matrix itself are usually dominants in the sense that they control the community, and these are usually plants which are in turn determined by the climate.

The biotic matrix may be analyzed ecologically in any of several approaches. It may be considered from the point of view of succession with developmental stages passing either through xeroseres or hydroseres to the climax community; it may be studied strategraphically and divided into societies or socies depending upon whether the community is developmental or climax in nature; or finally it may be considered aspectionally from the point of view of seasonal changes. Whether any or all of these methods are used, the permeant influents are less strikingly stratified, successional, or aspectional than the matrix organisms but rather tend to permeate all strata, all successional stages and all seasons in their search for food and shelter. The present study is concerned mainly with stratification in the biotic matrix, since it is within this area that most of the quantitative data are available. Only general information regarding succession and aspection can be given at this time. Furthermore, the present study is confined mainly to the aspect of greatest biotic activity included within the months of May to September inclusive.

Stratification studies were carried out at two stations representing the upper and lower elevations of the chaparral. Station 2 at the upper limit next to the montane forest was located near Aspen Grove, Mt. Timpanogos at an elevation of about 6,800 feet. Station 7 was established on Y Mountain east of Provo at an elevation of about 5,200 feet. Both stations were in the climax vegetation to be described in more detail below. Within each of these stations it was possible to recognize and sample three layer societies: (1) The ground layer society consisting mainly of the underground parts of living plants and decaying plant material together with the invertebrate animals associated therewith; (2) herb-low shrub layer society; and (3) the tall shrub layer society. Each of these societies will be considered in turn, and then the interrelationships of all will be discussed.

THE GROUND LAYER SOCIETY

Study of the soil organisms were carried out at both stations, but more detailed work was done at Station 7 on Y Mountain and the greater part of the present discussion will center upon that phase of the work. Most of the observations were made in the top two to four inches of the soil and under stones and other objects covering the ground surface. Experience has shown that it is in this stratum that the greatest number of organisms are to be found.

The soil types in which studies were made varied all the way from grayish soils of clay and fine gravel with comparatively little humus to rich black loam and dark leaf mould occurring to a depth of several inches under the scrub oak. At Station 7 quantitative samples were taken in open areas between clumps of oak and under the oak (Table 3). General col-

TABLE 3. Invertebrate population. Ground layer. Open area, Station 7, 1944. No. per M².

Mo. and Day	5-5	5-12	5-26	6-6	6-20	7-3	7-24	8-9	Av. per M²
Acarina	10	...	10	20	10	110	650	150	120.0
Formicidae	10	110	..	150	580	20	20	..	111.2
Araneida	10	20	10	...	10	10	...	...	7.5
Aptera	..	...	..	40	...	10	...	...	6.2
Coleoptera	20	...	..	...	...	...	...	...	2.5
Insect larva	..	...	10	...	...	10	...	...	2.5
Chilopoda	10	...	..	...	...	...	...	...	1.2
Thysanoptera	..	...	..	...	...	10	...	...	1.2
Collembola	..	...	..	...	...	10	...	...	1.2
Par. Hymenoptera	..	...	..	...	...	...	10	...	1.2
Hemiptera nymphs	..	...	..	...	...	...	10	...	1.2
Totals	60	130	30	210	600	180	690	150	255.9

Under Oak, Station 7, Data for 1945

	5-5	5-12	5-26	6-6	7-3	7-24	8-9	Av. per M²
Acarina	..	170	450	280	3210	3680	330	1160.0
Formicidae	..	10	20	10	140	690	50	131.4
Collembola	10	230	10	...	70	380	120	117.0
Insect larvae	10	40	60	10	30	20	80	35.7
Coleoptera	..	...	10	...	120	...	...	18.6
Pseudoscorpion	..	10	10	...	20	10	...	7.1
Diptera	10	...	...	10	10	10	...	5.7
Par. Hymenoptera	..	...	...	...	20	10	10	5.7
Araneida	..	...	10	...	20	...	...	4.3
Chilopoda	..	20	...	10	...	...	...	4.3
Diplopoda	..	...	...	30	...	...	...	4.3
Hemiptera	20	...	...	...	...	...	...	2.9
Mollusca	..	...	...	10	...	...	...	1.4
Totals	50	480	570	360	3640	4800	590	1641.4

lecting, mostly qualitative, was done under rocks and other objects on the ground surface.

Some observations were made, at times when samples were taken, of the microclimate during the summer. The results of these records are shown in Tables 4 and 5, which give an idea of the morning temperatures and the general trend of these tempperatures throughout the summer months of two years. While these data are far too fragmentary to be conclusive, two important features are indicated. First there is a general rise in temperature in both habitats beginning about the first of June and continuing until at least the middle of September; and

TABLE 4. Summer trend in soil temperatures at a depth of two inches. Wasatch Chaparral, Station 7, west facing slope. Data for 1944. Degrees F.

	Unshaded Area	Under Oak
May 5	56	54
May 12	60	53
May 18	51	50
May 26	53	50
June 6	61	52
June 20	63	56
July 3	64	55
July 24	76	69
August 9	82	73
September 14	83	75

TABLE 5. Typical soil temperatures at different depths during the warmest part of the summer. Station 7, Y Mountain. Data for August 10, 1945. 7:30 A.M. Degrees F.

	Unshaded Area	Under Oak
Surface	64.4	62.6
Two inches	66.2	60.8
Four inches	69.8	60.8
Six inches	71.8	60.8
Eight inches	73.4	60.8
Ten inches	71.6	60.8
Twelve inches	71.6	60.8

second, the temperatures of the soil under oak is, on the average nearly 10° F. colder than it is in the open.

Temperatures at varying soil depths from the surface to twelve inches were taken at intervals during the summer of 1945 at Station 7. All records were made at the approximate time that animal samples were taken in the early morning before sunrise. The results of typical records are shown in Table 5. From such fragmentary data it is impossible to draw many conclusions, but a few factors of great importance to soil organisms are indicated. The uniformity of temperatures in the soil under the protection of the oak below the two-inch level is striking. This is undoubtedly due in part to the shading effect of the oak and partly to the insulating action of the layer of dry leaves that covers the surface of the ground to a depth of about two inches. The soil in the open shows, on the other hand, a greater temperature variation with depth and clearly indicates the ability of the exposed ground to absorb quantities of heat during the daytime and to hold at least part of this heat at depths of six to eight inches throughout the night. This tends to confirm further an earlier statement regarding the importance of heat radiation in the chaparral community.

At depths of two to four inches where most of the organisms live, the daily temperature fluctuations in exposed soil must be considerable, while the same habitat under the oak is quite uniform. This may account in part for the great difference in population in the two situations which will be discussed later.

Unfortunately none but general observations are available regarding humidity and soil moisture in the microclimate. It is quite evident, however, that the microclimate of the soil under the oaks is much more humid, and uniformly so, than it is in open areas. This is due to the same factors, shade and insulation, that are responsible for temperature differences in the two.

Physical conditions of the ground layer which make possible the free movement of soil organisms and at the same time afford them protection from light and other disturbing features are of great importance. In open spaces the occurrence of loose rocks is very significant and the greater number of organisms are to be found under their protection. Under oaks the comparatively loose arrangement of

the leaf mould affords ample space for the free movement of organisms and at the same time protects them from intense light. On the other hand, the tightly packed soil of open areas affords relatively little movement space for organisms except those that are able to burrow.

The shrub and herb layers react upon the soil in several important ways. Soil binding properties of the roots of plants, especially grasses, are extremely vital to the maintenance of soil stability on steep slopes, and the significance of decaying plant material and shade in regards to the microclimate has already been pointed out.

For information pertaining to microscopic soil organisms the writer is indebted to Mrs. Desma H. Galway who made a quantitative study of the organisms in soil in open areas and under the oak. Her work which coincides with the writer's studies of the more primitive organisms but was carried out over a shorter period is freely used with her consent. The study was made during a period from April 1 to June 1, 1945.

With regard to bacteria and actinomycetes, Mrs. Galway found that they were more abundant in the open areas. She found about one million per gram in open soil as against 500,000 in the oak. The organisms were described but not positively identified and none were identical from open and oak areas.

The fungi, on the other hand were found to be more abundant in the soil under oak than in the open areas. There were about five times as many molds in the oak soil (50,000 per gram) than there were in the open soil (10,000 per gram). In the oak soil Penicillium was predominant with Murcor also present; in open areas Rhizopus, Aspergillus, and Fusarium were the most common genera represented.

The writer made quantitative studies in the upper two inches of soil under oak and in open areas. One tenth of a square meter of soil to a depth of two inches was removed and placed in a tight canvas

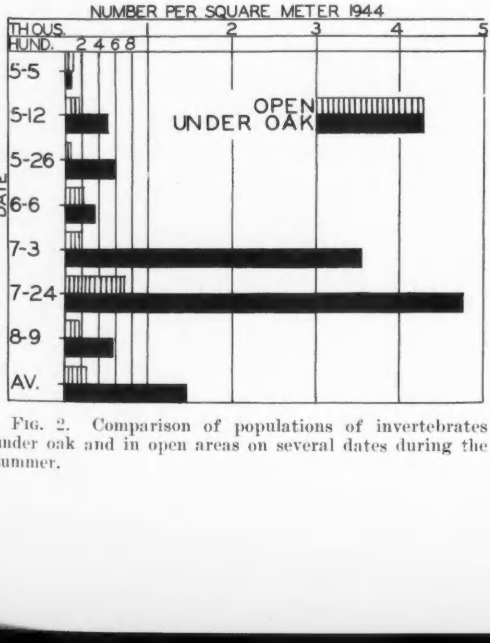

FIG. 2. Comparison of populations of invertebrates under oak and in open areas on several dates during the summer.

bag. It was then brought to the laboratory, carefully sorted for larger invertebrate and finally placed in a Berlese funnel from which the smaller species were collected in alcohol. The results of these collections are shown in Table 3 and Figure 2, and a check-list of animals identified at least to genus is given in Appendix C. Not so many samples were taken in 1945 but the results were similar.

Total populations show consistently greater number of invertebrates in the soil under oak than in the open. Populations in the open appeared to be more erratic than under oak during both seasons of collecting. In both years the rise in populations in the oak soil was slow in May and June but increased greatly in July and then began falling off in August.

In open soil, Acarina form about 47% of the average summer populations of all invertebrates, Formicidae come next with about 43%, and Araneida third with about 3%. The remaining groups occurred in negligible numbers. In the soil under oaks, Acarina were again the most abundant, forming about 77% of the average numbers for the summer. Formicidae comprise about 9% and Collembola about 7%. The small thief ant, *Solenopsis molesta validiuscula*, is very characteristic in this habitat.

The coactions of the complex assemblage of organisms forming for the most part a micro-community in the soil, especially in the rich, humus under the chaparral, are practically unknown. This in itself affords a most interesting problem in ecology. The Acarina which constitute such an important part of the population in this community are practically unknown taxonomically, and without a knowledge of their specific identity the ecologist is severely handicapped in any attempt to understand their biotic relationships. It is evident however, that the soil layer community is in the main a complete unit within itself. Its relationship with the other layers is similar to that between aquatic and land communities in general. The main contribution from the shrub and herb layers is the vegetable matter which falling into it forms the basis for the existence of the living organisms. Many of the animals require continuous darkness or semidarkness throughout their entire lives. This is true of the Acarina, Collembola, many spiders, insect larvae, millipeds and centipedes. On the other hand, some of the common inhabitants especially ants may invade the higher strata even in daylight for a portion of their food and also carry into the soil materials for the construction of their nests.

Most of the large invertebrates of the ground layer live under the protection of rocks. By far the most common of these animals are ants. In the higher elevations of the chaparral 85% of rocks turned over had ant colonies under them. The following species have been found:

Formica neogagates lasionides
Formica rufa obscuripes
Formica fusca gelida
Lasius latipes
Lasius niger sitkaensis

Lasius niger neoniger
Tapinoma sessile
Camponotus sansabeanus vicinus
Aphaenogaster uinta
Pheidole sp.
Monomorium minimum
Leptothorax nitens
Crematogaster lineolata
Solenopsis molesta validuiscula

Spiders also constitute an important part of the invertebrates found living under the protection of rocks. Records are available for the following most common species:

Neoantistea gosiuta
Tarentula kochi
Trochosa gosiuta
Schizocosa wasatchensis (most common)
Latrodectus mactans
Metaphidippus montanus
Gnaphosa muscorum
Drassyllus improvisus
Drassyllus apachus
Pardosa yavapa

The milliped, *Taiulus tiganus*, is common under rocks throughout the chaparral as is also the scorpion, *Vejovis boreus*. The most common centipedes are *Pokabius utahensis, Pokabius socius, Scolopendra polymorpha, Yobius haywardi*, and *Bothropolys permudus*. Isopods are not at all common but several colonies of *Porcellionides pruinosus* were found in the lower part of the chaparral on Y Mountain. Molluscs are likewise quite uncommon. A few specimens of *Oreohelix strigosa depressa* have been found, and a very few small bivalve shells have been noted.

Beetles constitute an important part of the invertebrate fauna under rocks. *Discoderus amoenus, Iphthimus sublaevis, Canthon corrvinus, Coniontis uteana, Galeruca externa* are the most common species that have been found.

Paper wasps quite frequently utilize the under side of rocks for the attachments of their nests. *Polistes fuscatus utahensis* and *Mischocyttarus flavitarsis* are the most common.

THE HERB-LOW SHRUB LAYER SOCIETY

The herb-low shrub layer is well defined throughout the chaparral. At the lower elevations it occupies the greater part of the total area between the scattered clumps of oak and other tall shrubs, but with an increase in altitude the tall shrubs come to cover more and more of the surface area until they crowd out the herbs and low shrubs almost entirely except for small patches of a few square feet. In such places the herb layer is limited to a few species of plants that are able to grow in the shade of the taller shrubs.

It is the herb-low shrub layer that has suffered most from overgrazing. Its original flora in many places has been almost completely obliterated and replaced by annual weeds such as June grass, tumble-mustard *(Norta altissima)* and sunflowers. The influence of man upon the animal inhabitants of this layer, indirectly through his influence upon the plants, can never be fully appreciated but it must have been of considerable importance. From meager descriptions of the flora as it occurred in the early days of settlement and studies of areas that have been under protection for a number of years, it seems quite evident that this layer was formerly a grassland. It is probable that the bunch grass, *Agropyron spicatum*, was the dominant species at least in lower elevations with *Poa secunda* also playing an important role. Both of these species are important dominants of the Palouse Prairie (Clements & Shelford 1939). Other grasses, which have been identified in this layer include *Poa longiligula, Poa curta, Poa pratensis, Oryzopsis hymenoides, Bromus tectorum, Bromus carinatus, Stipa lettermani, Stipa columbiana*, and *Festuca kingii*.

An analysis of the present flora of the herb-low

TABLE 6. Invertebrate population. Herb-low shrub layer. No. per M^2 Station 2. Data for 1940-41.

Month and Day	6-4	6-11	6-13	7-5	7-6	7-27	8-15	9-10	Av. per M^2
Cicadellidae	2	3	6	..	4	8	6	8	4.6
Par. Hymenoptera	2	5	..	8	2	6	6	..	3.6
Coleoptera	2	5	3	8	8	..	..	2	3.5
Aphidae	..	..	..	10	14	..	..	..	3.0
Diptera	..	1	1	12	4	3	..	..	2.6
Membracidae	..	..	8	8	..	1	..	..	2.1
Formicidae	4	..	..	6	2	2	..	..	1.7
Psvllidae	..	..	..	12	..	1	..	1	1.7
Hemiptera	..	2	..	2	8	2	..	..	1.7
Insect larvae	..	2	6	..	4	1	6	..	1.6
Araneida	1	..	2	..	..	2	6	1	1.5
Orthoptera	1	1	4	2	2	..	..	..	1.2
Other Hymenoptera	4	..	..	2	2	1	..	..	1.1
Neuroptera	..	..	..	..	..	1	..	..	*
Lepidoptera	..	1	..	..	..	..	..	..	*
Undetermined	3	..	4	..	..	..	..	..	*
Totals	19	20	34	70	50	28	18	12	31.3

*Less than one

Invertebrate Population

Tall shrub layer society Station 2
No. per M^2. Data for 1940-41.

Month and Day	1941	1940							Average
	6-4	6-11	6-13	7-5	7-6	7-27	8-15	9-10	
Par. Hymenoptera	4	10	..	12	..	32	4	..	7.7
Diptera	2	8	6	10	6	1	2	3	4.7
Cicadellidae	..	..	..	8	..	3	8	14	4.1
Araneida	1	10	8	2	6	3	..	2	4.0
Coleoptera	7	10	2	..	..	1	..	..	2.5
Formicidae	4	8	..	2	..	..	..	4	2.1
Insect larvae	..	12	4	..	..	..	..	..	2.0
Psyllidae	..	..	..	6	2	..	6	..	1.7
Membracidae	..	..	6	..	2	..	..	..	1.0
Unidentified	3	..	..	..	..	..	4	..	*
Hemiptera	..	2	..	..	2	1	..	..	*
Neuroptera	..	2	..	..	..	..	..	1	*
Lepidoptera	..	2	..	..	2	..	..	..	*
Aphidae	..	..	4	..	..	..	..	..	*
Other Hymenoptera	..	..	..	2	..	1	..	..	*
Totals	21	64	30	42	20	43	24	24	33.3

*Less than one

shrub layer indicates that it should most likely be considered as an ecotone between the valley grassland and montane forest communities. Few, if any, of its plants are confined strictly to the chaparral zone, and surely none is strikingly characteristic of it. A list of the more common plants of the herb-low shrub layer is given in Appendix D based upon the work of Tidestrom and on personal observation.

Populations of invertebrates in the herb-low shrub layer matrix are shown in Tables 6 and 7 and Figure 3. When the data for 1944 and 1945 are compiled for the two years for Station 7, there is shown a progressive increase in numbers from May until August and then a general decline in September. The figures for 1940-41 at Station 2 at a higher elevation are based upon fewer samples but indicate that the highest populations are reached in July. General observations tend to corroborate the idea

TABLE 7. Invertebrate population. Herb-low shrub layer Station 7. No. per M². Data for 1944.

Month and Day	5-5	5-12	5-18	5-26	6-6	6-20	7-7	7-14	7-24	8-9	8-16	9-7	9-14	9-21	Average per M²
Formicidae	...	2	...	8	25	22	40	30	37	27	62	64	7	19	24.5
Cicadellidae	3	...	...	6	23	9	7	20	12	5	20	1	2	15	8.7
Aphidae	...	...	...	...	...	...	...	...	...	15	14	5	15	50	7.0
Par. Hymenoptera	...	1	1	1	12	4	11	2	2	17	8	3	...	10	5.1
Psyllidae	...	...	...	1	...	...	4	2	...	...	51	...	3	2	4.5
Coleoptera	...	4	...	...	9	...	16	18	1	...	2	...	...	1	3.6
Hemiptera	2	...	...	1	20	14	1	...	2	...	2	2	...	5	3.5
Undetermined	...	...	...	...	...	12	...	...	13	8	...	2	...	11	3.2
Diptera	1	...	...	2	19	11	4	5	1	1	...	2	...	...	3.2
Fulgoridae	...	...	...	...	...	2	2	10	...	2	...	14	...	1	2.9
Orthoptera	...	...	...	...	...	1	2	5	4	2	2	...	1	11	1.3
Araneida	...	3	...	...	...	...	2	3	1	1	3	...	...	3	1.1
Lepidoptera	...	...	...	...	1	3	3	2	3	1	...	2	...	...	1.0
Membracidae	...	...	...	...	...	...	...	...	...	...	...	...	...	3	*
Tingidae	...	...	...	...	2	...	...	...	...	1	2	...	...	...	*
Apidae	...	...	...	...	...	...	...	...	...	...	1	...	...	...	*
Totals	6	10	1	19	111	78	92	97	76	80	167	95	28	131	70.7

Data for 1945

Month and Day	5-11	5-22	6-8	6-26	7-12	7-20	8-10	9-4	Av. per M²
Formicidae	4	6	2	10	43	69	54	8	24.5
Cicadellidae	11	15	8	21	16	6	7	1	10.6
Aphidae	..	..	24	13	..	2	..	1	6.0
Par. Hymenoptera	13	10	4	4	1	6	3	..	5.1
Diptera	5	8	4	10	..	1	5	1	4.2
Hemiptera	..	1	3	11	2	3	..	1	2.6
Coleoptera	..	..	3	1	7	2	..	..	1.6
Psyllidae	..	..	1	7	2	2	..	..	1.5
Orthroptera	..	..	1	6	1	3	..	1	1.5
Fulgoridae	..	..	..	..	..	..	7	1	1.0
Membracidae	2	..	..	..	..	..	..	..	*
Neuroptera	1	..	..	..	..	..	..	..	*
Lepidoptera	..	..	2	4	..	..	..	..	*
Tingidae	..	..	..	1	1	..	..	..	*
Insect larvae	..	..	..	4	..	..	..	..	*
Araneida	..	..	..	..	..	1	..	2	*
Thysanoptera	..	..	..	..	..	..	7	4	*
Totals	36	40	52	95	73	95	76	20	61.0

*Less than one

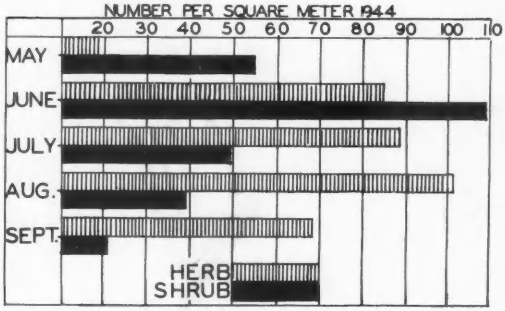

FIG. 3. Comparison of populations of invertebrates in herb and shrub layers of the Wasatch chaparral during the summer.

that peaks in summer invertebrate population are reached earlier in higher elevations.

At Station 7 ants were found to be by far the most abundant group in the herb-low shrub layer where they were found to constitute about 41% of the total invertebrate population for the summer. The minute black ant, ***Monomorium minimum***, appeared very frequently in samples, and the odorous ant, *Tapinoma sessile*, is also common. The acrobat ant, *Cremastogaster lineolata*, occurs often in considerable numbers in sample collections. At Station 2 at the upper edge of the chaparral ants made up only a little more than 5% of the total invertebrate population. Of the three species listed as common at Station 7, only *Tapinoma sessile* was found. The black ant, *Formica fusca gelida*, and *Formica neogagates lasioides* were the only species swept from the herb-low shrub layer.

Leafhoppers form a conspicuous part of the invertebrate population in the herb-low shrub layer at both Stations 2 and 7. At the former they were the most abundant invertebrates (about 15%) while at the latter they were second in importance (about 14%). The species represented at the two stations are shown below:

Station 2 (Elevation 6,800 feet)
Dikraneura carneola
Laevicephalus sp.
Phlepsius comulatus
Gypona sp.
Empoasca aspersa

Station 7 (Elevation 5,200 feet)
Dikraneura carneola
Deltocephalus grex
Deltocephalus dorsti
Laevicephalus abdominalis
Laevicephalus collinus
Eutettix latus
Ballana atridorsum
Macrosteles divisus
Macrosteles wilburi
Parabolocratus viridis
Psammotettix striatus
Acertagallia curvata
Stragania rufoscutellus
Empoasca neaspersa

Empoasca carsona
Xerophloea viridis
Gypona vexa

Orthroptera, mainly locusts and grasshoppers, form a conspicuous part of the matrix of the herb-low shrub layer. Sampling by the sweeping method probably does not give an accurate idea of the relative populations of this group since many of these more active insects are driven before the net. Specimens taken by sample sweeping are usually the less active nymphs. General observations indicate that grasshoppers are usually most abundant in waste spaces where there are considerable numbers of weeds. They are far less common where stands of bunch grass are dominant. The following species occur in the two stations:

Station 2 (Elevation 6,800 feet)
Scudderia furcata
Circotettix suffusus (?)
Circotettix tabula tabula (?)
Melanoplus mexicanus
Melanoplus atlanis
Melanoplus bivittatus
Acridium granulatum
Arphia frigida
Arphia simplex
Steiroxys pallidipalpus

Station 7 (Elevation 5,200 feet)
Arphia simplex
Hippiscus corrallipes
Melanoplus mexicanus
Mermeria bivittata
Hesperotettix viridis
Trimerotropis cyanipennis
Schistocerca shoshone
Circotettix undulatus
Leprus interior

Tall Shrub Layer Society

Forming the dominant vegetation as well as the most conspicuous aspect of the chaparral is the tall shrub layer. The predominant shrub is the Gambel oak *(Quercus gambellii)* with the Utah oak *(Quercus utahensis)* also present but in much smaller numbers. At the lower edge of the chaparral the squawbush *(Rhus trilobata)*, sumac *(Rhus cismontana)*, two species of hackberry *(Celtis reticulata,* and *C. douglasii)* mingle with the oak or more often form independent patches or clumps. At the upper elevations of the chaparral, a number of montane shrubs enter into the association, and mingle with the oak to form a dense thicket. These include service berry *(Amelanchier alnifolia)*, maple *(Acer grandidentatum)*, chokecherry *(Prunus melanocarpa)*, snow bush *(Ceanothus velutinus)*, and rose *(Rosa woodsi)*. In general aspect the climax chaparral appears at its lower border in scatered patches with extensive areas of herb-low shrub occupying the spaces between, giving to the whole a packland appearance. As elevations increase the tall shrubs come to occupy more and more of the area until finally at the upper limit, where chaparral merges with the montane forest, they form an almost continuous thicket.

In contrast to the costal chaparral in which the majority of the shrubs are evergreens, the Wasatch chaparral, except for one shrub (Ceanothus), is deciduous. The first appearance of leaves in spring varies somewhat from year to year, but it is usually about the middle of May before the buds burst at elevations of 5,000 feet and the first of June at the limits of elevation. By the last of October the leaves have again fallen, leaving the dull gray branches exposed for the remainder of the year.

Another conspicuous feature of the Wasatch chaparral is the presence of considerable patches of mahogany *(Cercocarpus ledifolius* and *C. montanus)*, antelope brush *(Purshia tridentata)* and cliff rose *(Cowania stansburiana)* all of which constitute important winter browse for deer. These shrubs, however, occupy rocky ridges and represent a stage in the xerosere rather than climax vegetation. The juniper (Juniperus) appears in scattered numbers in the Wasatch chaparral, but nowhere does it form the characteristic forests of other portions of the State.

The invertebrates which are associated with the tall shrub layer to form part of the biotic matrix, are characteristic of the layer and, in the main, set it apart distinctly from both the herb-low shrub and ground layers. Many of the species, particularly parasitic and gall-formers, are confined to one or another of the shrubs, and the various coactions within the community, most of which are little known, constitute a most remarkable study in themselves.

Most of the quantitative sampling of this study was confined to the deciduous shrubs, particularly the oak, since lack of time made it impracticable to study the seral development of the community. The results of the quantitative work are shown in Tables 6 and 8 and Figure 3. When the seasonal populations are considered it will be noted that the greatest numbers appeared in June in contrast to the herb-low shrub layer in which the populations were highest in August. However, a longer period of observation may alter this circumstance. There is often-times a tendency for individuals of a species to appear in very large numbers for a short period of time and then disappear. For example in 1944 a weevil *(Thricolepsis inornata)* appeared in very large numbers about May 26 and continued to about June 20 when it disappeared. At this same period a species of Tingidae was also very abundant and large numbers of parasitic Hymenoptera mainly of the genus Tetrastichus were common. The following year the weevil did not appear except in very small numbers, but the Tingidae and parasitic Hymenoptera were again abundant during a comparable season (Table 8).

The parasitic Hymenoptera are the most consistently characteristic invertebrates of the tall shrubs matrix. While other species often appear in greater numbers periodically, the Hymenoptera form the most intimate coaction with the oak, which is the dominant shrub and for that reason they are of unusual interest in any ecological consideration of the

TABLE 8. Invertebrate population. Shrub layer Society, Station 7. No. per M^2. Data for 1944.

Month and Day	5-5	5-12	5-18	5-26	6-6	6-20	7-7	7-14	7-24	8-9	8-16	9-7	9-14	9-21	Average
Coleoptera	1	1	2	57	106	16	1	1	2	...	2	...	1	1	13.6
Par. Hymenoptera	1	2	2	8	57	28	28	16	5	2	14	18	...	4	13.2
Formicidae	...	...	...	...	7	5	3	8	8	16	...	3	7	4	6.3
Diptera	1	1	2	8	17	21	3	4	1	1	6	6	1	...	5.0
Araneida	1	...	1	4	4	3	2	2	1	...	19	12	2	2	4.5
Tingidae	...	...	...	26	10	...	...	...	1	...	4	...	...	...	3.0
Unidentified	...	2	...	...	1	...	10	6	5	...	13	5	...	...	3.0
Cicadellidae	...	...	...	2	1	2	...	1	...	3	7	7	...	...	1.6
Membracidae	...	...	1	...	...	3	...	2	1	3	...	1	1	...	*
Psyllidae	3	1	...	...	2	1	...	...	...	...	1	1	1	...	*
Hemiptera	...	...	...	...	3	1	...	...	4	...	2	...	...	1	*
Orthoptera	...	...	...	...	...	...	...	...	5	4	4	...	...	...	*
Insect larvae	...	...	...	4	2	2	...	...	...	...	...	...	...	...	*
Lepidoptera	...	...	...	...	2	7	...	...	...	1	1	...	...	...	*
Aphidae	...	...	...	...	...	...	...	...	...	...	...	...	...	1	*
Neuroptera	...	...	...	...	...	...	...	...	1	...	1	...	1	1	*
Acarina	...	...	...	...	...	10	1	...	...	...	...	...	...	...	*
Fulgoridae	...	...	...	...	...	...	1	4	...	...	...	...	...	...	*
Totals	7	7	8	109	212	99	49	44	34	30	74	53	14	14	53.8

Data for 1945

Month and Day	5-11	5-22	6-8	6-26	7-12	7-20	8-10	9-4	Av per M^2
Diptera	71	17	9	5	2	5	4	3	14.5
Aphidae	..	14	1	2	1	16	1	..	14.3
Par. Hymenoptera	11	39	15	20	13	7	5	2	14.
Tingidae	..	..	..	46	39	3	..	..	11.0
Cicadellidae	..	14	1	7	6	..	2	..	3.7
Formicidae	..	..	..	..	9	..	..	8	2.1
Coleoptera	3	..	2	4	3	3	..	..	1.8
Araneida	4	..	1	3	3	..	..	4	1.8
Psyllidae	1	9	3	..	1	..	..	..	1.7
Tree Crickets	..	..	..	1	2	..	..	1	.5
Membracidae	..	2	..	1	..	..	..	..	*
Hemiptera	..	2	..	..	1	..	1	..	*
Insect larvae	..	3	..	..	..	1	..	..	*
Lepidoptera	1	1	..	..	1	..	..	..	*
Neuroptera	..	1	..	..	..	..	..	..	*
Apidae	..	..	..	..	1	2	..	1	*
Fulgoridae	..	..	..	..	1	..	..	..	*
Totals	91	102	32	89	83	37	12	19	58.1

*Less than one

community. Unfortunately the taxonomy of western parasitic Hymenoptera is practically unknown, so that in the majority of cases specific identification even of the species bred directly from galls was impossible. Until this classification is known we find it difficult to comprehend the precise coactions of the numerous species present, and can do little but guess at the relationships on the basis of what is known about the general habits of the several genera.

Two cynipid wasps, *Cynips villosa calvescens* and *C. hirta packorum*, are known to form leaf galls on *Quercus utahensis* (Kinsey 1929: 354, 418). Oak twig galls presumably formed by cynipids of the genera Andricus or Neuroterus are conspicuous objects. From these galls the writer has bred a species of Synergus, which is an inquiline with the gall maker and the following Chalcidoidea which are either parasitic or hyperparasitic on the gall insects:

Callimome rubenidis
Callimome warreni
Callimone maculipennis
Eupelmus allynii (Also known to be parasitic on Hessian fly)
Ormyrus sp.
Eurytoma sp.

The hackberry (Celtis) supports a number of leaf galls that are conspicuous and of considerable importance in the community. These are formed by psyllids (Hemiptera) of the genus Pachypsylla. The writer has bred *P. venusta* from large galls on the leaf petioles which cause the leaves to remain on the twigs all winter (Riley 1883: 157). The nymphs occur in great masses in these galls and are eaten extensively by the Woodhouse jay, and probably other birds. This bird is able to split the hard gall by striking it against a limb or rock with the beak. Adults of this psyllid appear in May. From the galls of *P. venusta* the writer has also bred a number of parasitic Hymenoptera belonging to the Chalcidoidea. These include *Amblymerus* sp., *Eurytoma* sp., and *Psyllaephagus pachypsyllae*. Three other species of psyllids that form galls on Celtis have also been identified. *Pachypsylla celtidis-vesicula* has been bred from leaf galls and adults captured in May. *P. celtidis-mamma*, known to form leaf galls (Riley 1883) appears in adult form in May and early June. One specimen of *P. celtidis gemma* was captured on June 8.

THE PERMEANT INFLUENTS

The vertebrate animals may be conveniently considered as permeant influents of the biotic matrix since they generally permeate all of the layer communities for one or another of their physiological needs, and their influence upon the communities is often marked. However, the distinction between permeant influent and biotic matrix is by no means exact and a separation of the two upon a vertebrate-invertebrate basis is by no means applicable in all cases. The student of biotic communities soon comes to realize that any biotic assemblage functions as a whole complex and not as independent parts, as was so clearly pointed out by Darwin in the closing paragraph of "The Origin of Species." An ecologist, attempting to describe a biotic community is confronted with many of the same organizational difficulties as the physiologist who must organize his treatment into chapters dealing separately with the several bodily systems, even though these systems do not function independently but as a complex integration.

Vertebrate animals, particularly the warm blooded types, are, on the whole, less strictly controlled by exacting biotic or physical factors of the community than are the constituents of the biotic matrix. Their requirements of particular food, specific climatic conditions, or exact circumstances for the critical repro-

ductive process are considerably more flexible. Whereas the scrub oak with its numerous invertebrate associates is confined to rather narrow physical conditions of the environment, and presents throughout all seasons the dominant aspect of the community, the majority of the vertebrate inhabitants of the chaparral are either transitory, seasonal or else are no more confined to this community than they are to one of several others.

Reptiles

The reptilian inhabitants of the Wasatch chaparral belong essentially to the desert shrub and grasslands of the valleys, and in nearly all cases reach their altitudinal limits within this community. Their distributional relationships with the chaparral and its bordering communities are indicated in Figure 4.

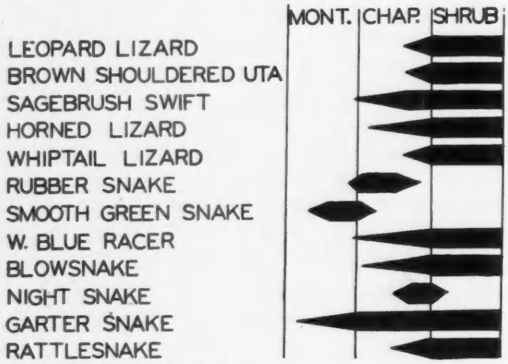

FIG. 4. Distribution of reptiles in the chaparral and the adjoining montane forests and desert shrub.

In the main they are confined to the ground layer community, although the sagebrush swift often climbs into shrubs and the blue racer and grass snake frequently rest upon the branches of the taller shrubs. Several of the snakes in particular are so rare that their exact distribution and ecological significance are not clearly understood. The grass snake *(Opheodrys vernalis)* appears to be more nearly characteristic of the lower montane than it is of the chaparral. However, it may seek the warm chaparral covered exposures where it hibernates under rocks. During the month of May, particularly during stormy or cold intervals, it may be found in considerable numbers coiled under rocks, frequently in company with the rubber snake *(Charina bottae)*. This latter species appears to be the most nearly confined to the chaparral of any of the reptiles but it is so rare that its distribution is not well known.

The sagebrush swift *(Sceloporus graciosus graciosus)* is by far the most conspicuous reptile of the chaparral. Woodbury & Woodbury (1945) have studied life history and reproductive cycles in this species. These writers state that the young lizards emerge from hibernation about the first of April and breed soon afterward. Eggs are laid from June 16 to July 12, and the period of development in the soil occupies about two months. Adults go into hibernation about September 22 and the young a few weeks later. Several studies on the food of this lizard (Gertsch & Woodbury 1930, Knowlton *et al.* 1936, etc., Pack 1921) in the vicinity of this study indicate that the greater part of the food consists of Arthropoda taken from the ground layer community. Gertsch & Woodbury listed a number of spiders eaten by this lizard. Pack, who studied seventy specimens taken in the chaparral northeast of Salt Lake City in August found that the red-legged locust *(Melanoplus femur-rubrum)* was the most common food while ants were the next most abundant item in the diet. It appears probable that *Melanoplus m. mexicanus* is more commonly used in the area of the writer's study since it is by far the most abundant grasshopper. Population studies were made in California by Stebbins (1944). A list of the reptiles known to occur in the Wasatch chaparral is given below:

Crotaphytus wislizenii (Baird & Girard) Leopard-Lizard
Uta stansburiana stansburiana (Baird & Girard) Brown-shouldered Uta
Sceloporus graciosus graciosus (Baird & Girard) Sagebrush Swift
Phrynosoma orbiculare ornatum (Girard) Horned Lizard
Eumeces skiltonianus skiltonianus (Baird & Girard) Western Skink
Charina bottae (Blainville) Rubber-snake
Opheodrys vernalis blanchardi (Grobman) Smooth Green-snake
Coluber constrictor mormon (Baird & Girard) Western Blue Racer
Pituophis catenifer deserticola Stejneger Blow Snake
Hypsiglena ochrorhyncha deserticola Tanner. Night-snake
Thamnophis ordinoides vagrans (Baird & Girard) Wandering Garter Snake
Crotalus viridis lutosus (Klauber) Great Basin Rattlesnake

Birds

(Appendix A, Figure 5, and Tables 9, 10 and 11.)

The avian fauna of the chaparral constitutes one of the most interesting and ecologically significant constituents of the community. The complex role played by birds presents the ecologist with numerous problems, the greater part of which are, at the present time, only partially understood. Unlike the mammalian, reptilian, invertebrate and plant inhabitants which are relatively stable at all seasons either in active or dormant states, the populations of birds are, in the main, quite seasonal with only a relatively small number of species consistently present throughout the year. This state of affairs is, of course, characteristic of any community where birds are present, but it serves well to emphasize the fact that the ecologist is confronted with a somewhat different problem in the analysis of the community than is the student of pure faunistics. From a faunistic point of view the breeding population is generally taken as a criterion for the analysis of the avian

characteristics of the community. While a certain set of environmental conditions may consitute an optimum condition for *propagation* it may not be optimum or even tolerable for *perpetuation,* and of course the one is as vital as the other is in the survival of the organisms and of the community.

TABLE 9. Frequency of occurrence of more common birds found in the Wasatch Chaparral, May 1 to August 31, together with principal nesting and feeding layer communities. Data compiled from 30 field trips.

	Percent of times noted	Nesting layer	Principal feeding layer
Spurred Towhee	93.3	Ground	Ground
Virginia Warbler	80.0	Ground	Shrub
Black-headed Grosbeak	73.3	Shrub	Shrub
American Magpie	73.3	Shrub	Ground
Broad-tailed Hummingbird	56.6	Shurb	Herb
Green-tailed Towhee	53.3	Ground Shrub	Ground
West. Mourning Dove	50.0	Shrub Ground	Ground
West Red-tailed Hawk	50.0	Ground	Ground
Woodhouse Jay	50.0	Shrub	Shrub
Lazuli Bunting	36.6	Shrub	Shrub
West. Chipping Sparrow	20.6	Shrub	Shrub
Steller Jay	20.6	Shrub	Shrub
Prairie Falcon	20.6	Ground	Ground
Black-capped Chickadee	20.6	Shrub	Shrub
Western Robin	20.6	Shrub	Ground
Sparrow Hawk	20.3	Ground	Ground
Gray-headed Junco	20.3	Ground	Ground
Rock Wren	20.3	Ground	Ground
Macgillivray Warbler	20.3	Shrub	Shrub
Ring-necked Pheasant	20.0	Ground	Ground
Red-shafted Flicker	20.0	Shrub	Ground
White-throated Swift	20.0	Ground	Aerial
Orange-crowned Warbler	16.6	Ground	Shrub
Sharp-shinned Hawk	13.3	Shrub	Shrub
Nuttall Poor-will	13.3	Ground	Aerial
Turkey Vulture	13.3	Ground	Ground
Audubon Warbler	10.0	Shrub	Shrub
Canon Wren	10.0	Ground	Ground
West. Warbling Vireo	10.0	Shrub	Shrub
Ruffed Grouse	6.6	Ground	Ground

Table 10. Populations of birds in the Wasatch Chaparral during the summer aspect. Expressed in numbers per hectare.

	1944								1945				
	May				June		July		May		June		July
	5	12	18	26	6	20	3	14	11	22	8	26	12
American Magpie	8	8	6	7	5	8	3	2	7	1	5	5	7
Spurred Towhee	5	6	4	3	8	4	5	5	7	2	6	7	2
Virginia Warbler	1	2	4	2	5	2	..	..	7	2	1	1	1
Bl.-Headed Grosbeak	..	..	2	1	1	2	..	3	..	1	..	2	6
Woodhouse Jay	..	..	3	..	..	1	..	4	2	..	2	2	3
W. Meadowlark	..	1	1	..	..	2	6	..	..	..	..	1	1
Lazuli Bunting	..	5	..	..	1	..	..	..	..	..	..	..	1
Broad-tailed Hummingbird	..	1	3	..	..	..	..	..	2	3	..	2	..
Other species	19	7	9	8	13	8	7	2	3	2	2	1	13
Totals	33	30	32	21	33	27	21	16	28	11	16	21	34

TABLE 11. Summer populations of birds of the Wasatch Chaparral compared with adjacent montane and desert shrub communities.

	Av. No. per Hectare
Lower Montane Aspen (Subclimax)	28.0
Upper Montane Subclimax	25.0
Wasatch Chaparral (Climax)	24.8
Upper Montane Climax	16.5
Lower Montane Climax	15.5
Desert Shrub Shadscale (Fautin, 1946)	1.0
Desert Shrub Greasewood (Fautin, 1946)	2.7

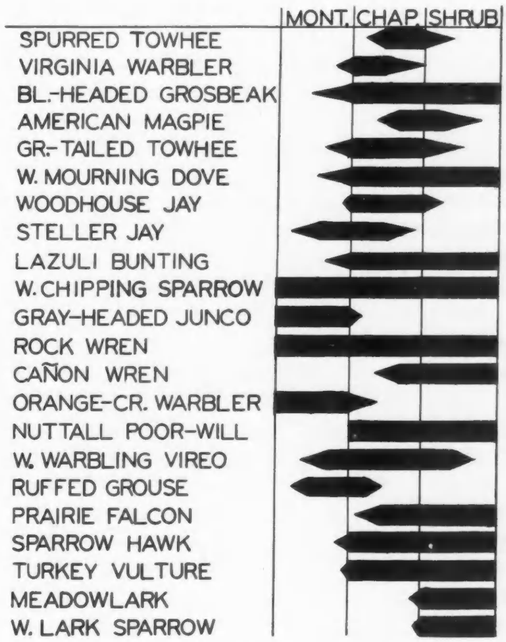

FIG. 5. Distribution of the more common breeding birds in the chaparral and adjoining montane forests and desert shrub.

The ecologist is not only interested in the effect of the environment upon the organism but he is also concerned with the influence of the organism upon the environment (reaction and coaction). For example, the Montana junco *(Junco oreganus montanus)* breeds in eastern Oregon and Washington, northern Idaho, northwestern Montana and northward (Miller 1941: 257) and may be said to be "characteristic" of that area. Yet many thousands of these birds winter in the Wasatch chaparral where they spend at least nine months of the year as compared to not more than two months in the nesting area. Furthermore, in winter when these birds form into large flocks, their coaction upon a favorite locality may be more ecologically significant and characteristic than would be the case were they territorially scattered over the breeding zone.

On the other hand, the Virginia warbler (*Vermivora virginiae* Baird) insofar as the Wasatch area is concerned, breeds mainly in the chaparral where it is present in fairly large numbers for about eighteen weeks of the year. During the remaining 34 weeks it is either enroute to and from the wintering grounds in Mexico or resident in the wintering grounds themselves. While this species may be considered "characteristic" of the Wasatch chaparral, its total influence upon the community may be of only minor ecological significance.

With these factors in mind, the ecologist, in attempting to evaluate the various avian constituents of any community, must understand such factors as size of the individual, population of the species, time of sojourn in the community, and concentration of flocks. All of these must be weighed one against the other in evaluating the effect of any one kind or group of similar species upon the total ecology of the community.

Therefore, considering the birds as a whole as community influents, the avian population (Appendix A) of the Wasatch chaparral may be arranged into the following groups in the order of their ecological significance:

1. Permanent residents. Influents in all seasonal aspects.
2. Winter visitants only. Influents of the winter aspect, which is in general the period of dormancy of the biotic matrix.
3. Summer residents only. Influents of the period of greatest activity in the biotic matrix.
4. Migrant and local transients. Temporary influents of the vernal and autumnal periods of transition and accidentals which may appear at any season.

From the point of view of species, these several aspectional groups are numerically fairly evenly divided as follows:

Permanent residents only	26 species
Winter visitants only	20 species
Summer residents only	30 species
Migrants and local transients	31 species
Total	107 species

Indications of the aspectional features of the mountain avifauna of this area have been given by the author in a previous paper (1945: 76). While there is no clear cut line of demarcation between the avian seasons, the field worker soon comes to recognize the general periods, and it is proposed herein to elaborate further upon these aspects as they apply to the ecology of the Wasatch chaparral.

From an ecological point of view, as indicated previously, the winter aspect is probably the most important since it occupies the greater part of the year from about the middle of October to the latter part of April. While there are fewer kinds of birds in the community during this period, the total number of individuals is equal to or greater than it is during the nesting season. Futhermore, the tendency for many of the smaller birds to form into large flocks and concentrate their feeding activities in restricted areas must undoubtedly greatly influence the community in those places.

Certain features of the winter aspect are of paramount interest and importance:

1. The climatic features as indicated previously are especially conducive to the wintering of birds, particularly with westward slopes, since large areas of ground are almost continuously exposed. Even after heavy snowfall, south and west slopes are usually uncovered within a matter of hours or a few days at the most, while the valley and higher slopes may remain covered for much longer periods if cold weather follows immediately after the snowfall.

Kendeigh (1945) has shown that the survival time of English sparrows without food is shortened materially as temperature decreases. Thus, a heavy snowfall to hide the food, plus cold weather which customarily follows, must be fatal to species that gain their food largely from the ground. The superior advantage of steep slopes of the foothills where the warming power of the sun is fully utilized, is, therefore, of great advantage to the wintering birds. Hayward (1935) has previously contrasted the winter bird life of Bear Lake Valley, Idaho-Utah, and Utah Valley, and shown that in the former case the smaller numbers of ground feeding birds must be attributed to long periods when the ground feed is unavailable because deep snow covers the ground. While the colder climate of Bear Lake Valley may on first thought be considered the direct limiting factor, Kendeigh (1934) as well as other experimenters, has shown that when properly fed, adult birds can survive extremely low temperatures, and that the mechanisms for maintaining high body temperatures in cold weather is very effective providing energy materials are available.

2. The available sources of food is another important ecological factor of the winter aspect. The larger predatory species, the most important of which are the golden eagle, goshawk, red-tailed hawk and horned owl, prey upon the desert jackrabbit and cottontail. During the early and late portions of the season, marmots, rock squirrels and chipmunks are also utilized. Some of the large predators customarily feed over large areas, probably at least ten miles in diameter, so that they may gain part of their food from adjacent communities.

The contributions of the shrubs to the winter feed of birds is extremely important. On the lower edge of the chaparral the hackberry appears to be the most important. Various psyllid galls, filled with nymphal forms previously discussed, persist on dead leaves, many of which remain on the shrub throughout the winter. These are utilized especially by the Woodhouse jay which is able to break open the hard galls with the beak and remove the food. It is likely that this food is also utilized by Stellar jays and flickers but direct evidence of this is lacking. The fruit of the hackberry is likewise an important supply of winter food. Robins, Stellar and Woodhouse jays, Townsend solitaires, flickers, Bohemian and

cedar waxwings, and spurred towhees make wide use of these nutritious fruits which remain on the shrubs throughout the winter.

Contributions of the oak to the winter bird food is chiefly through the acorns. However, they are shed in early autumn and must be gleaned mostly from the leaf layer under the shrubs. While they are used mainly by mammals, jays may also feed upon them to a large extent. Twig galls are very abundant on the oak, but it is doubtful if they are used to any extent by birds. Mountain and black-capped chickadees are the chief twig feeding species found in the chaparral in winter, but they appear to depend more upon the readily available dormant insects or eggs that are attached to the surface or under loose bark.

At the upper limit of the chaparral, the serviceberry may, in certain favorable years, supply a goodly source of winter food. On these occasions the berries dry and remain attached to the twigs throughout the winter. Large flocks of robins, and smaller numbers of Townsend solitaires as well as flickers are known to feed upon these berries. Winter buds of many of the shrubs are eaten by the ruffed and dusky grouse, Rocky Mountain pine grosbeak, and western evening grosbeak.

By far the great majority of wintering birds obtain their food directly from the surface of the ground. Spurred towhees, pheasants and quail feed largely under the protection of the shrubs, especially oak, and commonly scratch among the leaves for food. Juncos of several kinds, pine siskins, house finches, white-crowned sparrows, leucostictes, and goldfinches feed in open spaces and utilize the shrubs mainly as perches to rest or seek protection from predatory mammals.

The exact nature of the food of these ground feeders has been studied by Frost (1947), and it is evident that it is largely seeds of the herb layer. While some dormant invertebrates are available to the species that scratch in the oak leaves, the great majority of these species spend the winter under rocks or deep in the ground where they are not available to birds. Careful watching of the feeding process of these flocks of Fringillidae indicates that there is plenty of food on the surface of the ground easily accessible without much effort on the part of a bird.

On the few occasions when there is a complete coverage of snow there are usually sufficient herbs, particularly sunflowers and grasses, projecting above the snow to provide food until the ground is bare again.

4. The degree of aggregation among wintering birds and their consequent movements constitutes an important feature of the winter aspect. In common with the habits of the species elsewhere there are all degrees of aggregation from single individuals that show little tendency to associate with their own kind or other species to large flocks of a thousand or more individuals. Considerable study of the social behavior of birds, especially in complete or semi-confinement (Allee 1936) has been made, but the study of bird flocks in nature has been fraught with difficulty on account of the problem of keeping track of individuals.

Outstanding features of the winter social behavior of the birds of the Wasatch chaparral may be indicated as follows: (1) There is a general tendency for the flocks to occur in the mouths of canyons and the bottoms of canyons and to avoid open flats or ridges. (2) The flocks are almost invariably mixtures of several species, characteristically juncos of several subspecies, pine siskins, robins, Woodhouse jays, and chickadees. (3) From the places of concentration, which are largely night roosts, the flocks tend to move out during the feeding period into surrounding areas. This is a slow drifting movement a few yards at a time or from bush to bush and usually in an uphill direction along the bottoms or sides of canyons. Less is known of the return flight, but it appears to be more direct to the roosting area. (4) The Spurred towhee, which is the most characteristic species of the chaparral, does not participate to any noticeable degree in flocking or in the drifting movements indicated above. During the winter they remain largely solitary and presumably confine their foraging to a small area within the confines of one or two clumps of oak. (5) Woodhouse jays tend to mingle with other species including the Stellar jay. They are seldom solitary but occur in groups of two to five individuals. (6) Chickadees, both Nevada black-capped and mountain, also like the company of other species but drift more rapidly. They invariably occur in pairs or small groups up to six. (7) Large flocks of certain species may congregate in areas favorable for feeding during certain winters. During the winter of 1944-45 great flocks of robins occurred in the upper part of Rock Canyon where there was an abundance of dried service berries. In 1945-46 there were no berries and no birds in the same area. A flock of western crows estimated at a thousand or more established a roost in Slide Canyon east of Provo during part of the winter of 1945-46. They fed upon hackberries during their stay in that area.

5. Nesting activities during the winter aspect are confined to certain permanent residents (hawks and owls) and are limited to the last few weeks of the season. While this period is generally thought of as early vernal the general aspect of the community at this season is distinctly winter. The chief environmental variant is the lengthening period of daylight which is undoubtedly a more potent factor in the breeding activities of the birds than temperature. The golden eagle may begin nesting as early as the middle of March (Bee & Hutchings 1942) and often chooses sites on cold northfacing cliffs where there is no direct sunshine and with several feet of snow all about. The Montana horned owl also begins nesting activities in mid March when winter conditions still are prevalent, and the red-tailed hawk and ferruginous rough-leg breed during the latter part of March and the fore part of April.

Several members of the crow family commence breeding during the latter part of the winter aspect. The American magpie begins to nest in early April

and the American raven, which breeds in limited numbers in the canyons of the chaparral community, nests at about the same time. According to data furnished by Bee & Hutchings (1942) the Woodhouse jay does not breed until late April or early May.

The summer aspect of the avian population, extending from about the last week in May to about the middle of August, has as its chief characteristic the nesting of the great majority of the summer residents and the maturing of the young. At this season there are more species of birds present in the chaparral, but the flock formations are not in evidence until the last few weeks. Even though the flocks are broken up, and most of the species that form them during the winter aspect have moved into other communities to breed, there is still a decided tendency to gather in canyons rather than to scatter evenly throughout the community.

The coaction of the summer residents with the biotic matrix assumes a different relationship than does the winter aspect. This period, extending from about the last week of May to mid July, coincides with the greatest activity of the invertebrates of the community, and the period of growth of the young birds corresponds with the highest populations of invertebrates which occurs during the latter part of June and the first three weeks of July. Studies of the food of the chaparral birds, to be published in detail later, clearly show, as would be expected, that in summer the invertebrates form the major item of food of the avian population.

Contributions of the several layers of the biotic matrix to the food, nesting places and materials, and protection for the summer bird residents is a factor of great ecological interest. It is well known that birds are in the main permeants in all the layer societies represented in the community. These relationships have been previously described by the writer (1945:68) for the coniferous forests. This same general condition prevails in the chaparral.

Several of the more common birds utilize the ground layer under oak or other shrubs for nesting sites but make use of the shrubs for other purposes. The spurred towhee builds its nests on the ground well within the protection of the oak or the other dense shrubs and also gains much of its food from that layer by scratching in the dead leaves. The shrubs, themselves, are used mainly as perches for singing. When singing birds are disturbed they invariably seek the ground for protection rather than seeking higher branches of the shrubs. In this respect the towhee well exemplifies a habit characteristic of shrub dwelling birds in general as opposed to forest dwellers that tend to seek the tops of the trees for protection.

The habits of the spurred towhee are shared also by the green-tailed towhee, although the latter species often builds its nests in the shrubs a few inches from the ground.

An account of the nesting habits of the Virginia Warbler in Colorado has been given by Bailey & Niedrach (1938). It is characteristically a chaparral species during its period of residence which extends from about May 1 to September 20 in the Wasatch chaparral. Its nests are generally placed in the roots of the oak and well hidden by fallen leaves and herbaceous growth. When they first arrive in May the birds are quite conspicuous in the oaks before the leaves have gained much growth, and at that time they can be easily flushed from bush to bush. However, when the leaves are well out and the nesting is underway, it is next to impossible to see the birds, let alone dislodge them from the particular oak clumps in which they live. The only indication of their presence is the occasional song or the excited chipping characteristic of the species.

The tendency to rely for protection upon the dense cover of a thicket rather than to flee from bush to bush at the approach of danger is also characteristic to a lesser degree of the Woodhouse jay. This species builds the nest eight to ten feet up from the ground, but the birds themselves often hide in or near the roots of the shrubs. Even in winter, without benefit of the leaves, these birds can remain effectively hidden among the branches and can be dislodged only with difficulty. However, if the jays are surprised in the open they seek protection in flight and remain a safe distance from the intruder.

The relationship of the American magpie to the biotic matrix of the chaparral is mostly with the shrub layer during the nesting season. Nests are constructed long before the leaves appear and are conspicuous because of their bulk. By the time the young are hatched, however, the nests are well concealed, and both the adults and young tend to remain close to the protecting influence of the dense foliage. When the young are able to fly the adult and young magpies form large flocks, usually feed in the open, and remain well out of reach of any observer.

Two other common species, the black-headed grosbeak and lazuli bunting, share with the above mentioned species the general habits of staying close to the dense cover of the shrubs. Both species arrive in the spring only after the leaves are well out. Males of the black-headed grosbeak usually remain well hidden even while singing, and the female rarely exposes herself after nesting begins. The male lazuli bunting tends to sing from exposed perches but he is difficult to see from above. The female remains very close to the protection of the shrubs. Most of the food of both these species is gained from the shrub layer and the nests are likewise built in shrubs.

Nesting and feeding relationships of the thirty most common species of chaparral summer resident birds to the layer communities are indicated in Table 9. It will be noted from this table that the nesting sites and feeding areas are about equally divided between the shrub and ground layers. The contributions of the herb layer to the bird inhabitants is quite difficult to separate from the ground. This layer provides concealment for certain of the nests and many of the seeds, and invertebrates drop

to the ground or are eaten directly from the plants. But the herbs are too fragile to support the weight of the nest or the bird in the majority of cases.

The greater part of the work on bird population has been done during the summer aspect which is considered to be the period of greatest stability. Accurate counting of birds in the chaparral was quite impossible on account of the dense cover and secretive habits of the birds characteristic of the community. The ordinary method of cruising employed in open forests or prairies undoubtedly indicated only a small proportion of the birds actually present especially in the dense growth at higher elevations. Careful watching of relatively small areas from some vantage point during the most active nesting period seemed to give the most nearly accurate results, especially in the dense chaparral near its upper border. Cruising over larger measured areas yielded fairly good results in the open stands of chaparral near the lower border.

Results of several censuses taken in 1944 and 1945 between 8:00 and 9:00 A.M. are indicated in Table 10, and comparisons with populations in various communities of the montane forest are shown in Table 11. The data are too fragmentary to be conclusive, but when the average count is taken it is surprising how close the chaparral population approximates the numbers in the subclimax stages of the montane forest. These figures coincide with general impressions from field work that the breeding bird population of the chaparral climax is considerably higher than it is in the climax montane forests and very much higher than it is in the alpine climax.

Comparative censuses in the developing stages of the chaparral have not been made. Population trends of the summer aspect are not significantly indicated in the figures, but it is doubtful if there are any great differences throughout this period. The temporary increase occasioned by the new broods of young is tempered by the gradual shift of the birds into surrounding communities during the latter part of the summer.

The vernal and autumnal activities of birds within the Wasatch chaparral are of considerable interest and significance on account of the particular climatic and geographical position of the community. Vernal activities begin about the last of April and extend well into May. They are characterized by the following features: (1) Permanent residents, many of which began nesting during the winter aspect, are well along with the rearing of young or at least have selected territories and begun to nest at this season. The spurred towhee begins to sing about April 1 and has been noted building the nest as early as April 21. (2) There is a considerable fluctuation in poulations of many of the wintering birds because of local weather conditions. Such species as the townsend solitaire, gray-headed junco, white-crowned sparrow, golden-crowned kinglet and black leucostiete disappear during intervals of good weather, but reappear during the periodical spring storms which temporarily drive them down again from higher elevations. (3) Migrants enroute to higher elevations or more northern latitudes frequently appear in the chaparral. During the first part of May the western tanager moves through the chaparral on its way to the montane forests. The Audubon warbler also migrates through the chaparral at this season and breeds in the upper fringes of it as well as in the montane forests. Orange-crowned warblers appear in the chaparral in large numbers in May but apparently breed in the montane forests. However, the breeding status of this species is not well understood in this area. Most any of the species included in the foregoing list of migrant and local transients might appear during this period of vernal shift.

Autumnal activities that begin about the last week in July and extend through August and September are in certain respects a reversal of the vernal movements, but also have certain characteristics of their own. (1) After the young have attained sufficient maturity to fly, there is a general tendency in some species to drift up the mountains to higher elevations. This habit is most noticeable in the green-tailed towhee, but is also characteristic of the Macgillivray warbler, vesper sparrow, and Brewer sparrow. (2) There is a tendency toward the formation of flocks. This is most apparent in the magpie, which begins to flock by mid-July, and the Brewer blackbird, which often visits the chaparral in flocks during this period. (3) Finally, there is a transition through the chaparral of a number of species enroute to the wintering area and an arrival of the migrants that are to winter in the chaparral itself. Knowledge of the transients is limited because of lack of sufficient field work, but the more common species include Hammond flycatcher, western gnatcatcher, Calaveras warbler, northern pileolated warbler, and the rufous hummingbird.

The distribution of birds of the chaparral with relations to succession and the adjacent communities will be considered in another section of this paper.

MAMMALS

(Appendix B, Figure 6 and Tables 12, 13, and 14.)

TABLE 12. Populations of mammals, chipmunk size and smaller, at stations in the upper part of Wasatch Chaparral (el. 6,800 ft.) based on trapping 0.2 hectare, square plots at intervals for 5 consecutive nights and days. Expressed in numbers per hectare. Data for 1939-1941.

	June	July	August	Average
Peromyscus maniculatus	25	55	35	38.3
Eutamias minimus	5	15	30	13.3
Eutamias quadrivitattus	0	5	5	3.3
Clethrionomys galei	0	5	0	1.6
Totals	30	80	70	56.5

TABLE 13. Populations of mammals, chipmunk size and smaller, lower Wasatch Chaparral (el. 5,500 ft.) based on trapping 0.2 hectare plots at intervals for 5 consecutive days and nights. Expressed in numbers per hectare. Data for 1946.

	April	May	Average
Peromyscus maniculatus	115	90	102.5
Peromyscus truei	5	0	2.5
Reithrodontomys megalotis	0	10	5.0
Eutamias dorsalis	8	7	7.5
Totals	128	107	117.5

TABLE 14. Populations of *Peromyscus truei* on an isolated plot of an early xerosere stage, Rock Canyon, Wasatch Mountains. Data for 1945-1946. Area: 0.15 hectare.

	No. trap nights	No. Specimens		
		Females	Males	Total
November	1	1	6	7
December	5	15	18	33
January	5	5	11	16
February	4	3	6	9
March	9	7	9	16
April	4	0	1	1
Totals	28	31	51	82

NOTE: A total of 21 specimens of other species of mice was taken from this plot during the same interval.

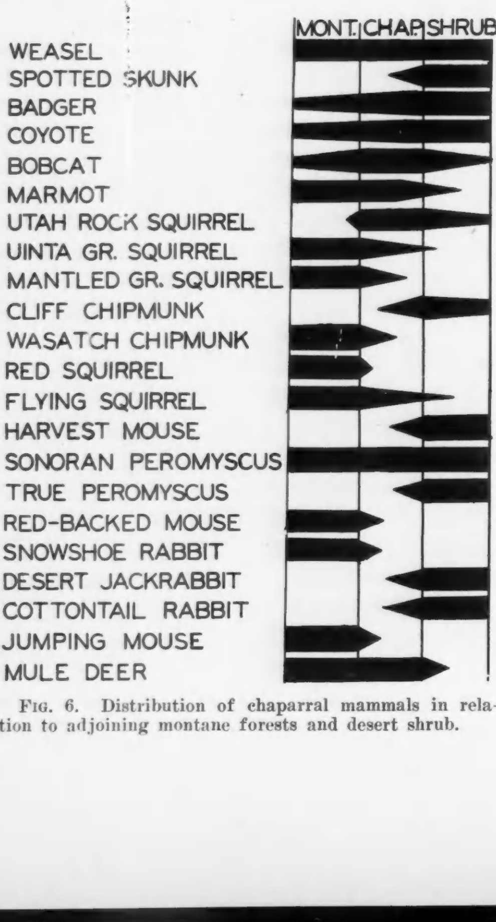

FIG. 6. Distribution of chaparral mammals in relation to adjoining montane forests and desert shrub.

The mammalian population of the Wasatch chaparral constitutes an important group of influents with many features of ecological significance. Aspectional variations in the mammals are of course not so striking as they are in the birds. There is an insignificant amount of hibernation among the chaparral mammals and only the mule deer and American wapiti are important as migrants. The American wapiti has been introduced on Mt. Timpanogos and Mt. Nebo but only a very few animals remain on Timpanogos and the writer has made no study of the herd on Mt. Nebo.

Of all the mammalian inhabitants of the chaparral the mule deer is probably the most important influent. Several features of the deer population are of ecological significance. (1) Although deer are present throughout the year they are much more abundant during the winter aspect when they utilize the community as a winter feed ground. (2) There is a definite tendency for concentration in certain areas from long established habits, but these areas usually support a good supply of favorite winter browse.

The autumnal drift or migration of deer into the chaparral from the montane forest depends somewhat upon the deposit of snow, but it usually occurs mainly during November. In the spring the upward movements follow closely, in the main, the retreat of snow, but the animals are found in large numbers on favorite winter feed grounds on the west face of Mt. Timpanogos as late as the last of May. On the other hand considerable numbers of deer were present in the high Uinta Mountains as early as June 6 when there was still much snow and practically no growth of new vegetation.

This up and down movement is quite irregular since there is little indication of mass movements at fixed times. The spring drift is occasioned by the tendency of the pregnant females to scatter out and remain in general at lower elevations for the birth of the fauns in June. The bucks tend to drift to higher elevations and often remain in small herds during the summer. Autumnal movements consist of a gradual gathering into favorite winter feeding grounds as food becomes less available at higher elevations.

The extent to which deer drift into high elevations during the summer is modified greatly by the total populations and the crowded conditions in the winter feed grounds. Those of us who have had these activities under observation for a number of years have noted a decided increase in summer deer populations at high elevations where they were formerly rare. This situation is mainly attributed to crowded conditions at lower elevations where competition for food and territory is an important item. This circumstance may result in an added burden upon the chaparral due to a longer sojourn as well as to increased numbers.

In common with many areas of the west in recent years, the wintering grounds of the deer in the Wasatch chaparral have been severely effected by the

concentrated feeding of increasing numbers of animals in favored areas. This important coaction is due in part to the reduction of predatory animals and in greater part to the protection of does by game laws and the general prejudice of local hunters against killing does. There is little indication of the abundance of deer previous to the advent of the white man, but it appears quite unlikely they were as abundant as they are today. In that day they were preyed upon by carnivors and Indians, neither of which apparently made any distinction between the sexes. With the first appearance of permanent white settlers there were few restrictions on hunting with the result that both does and bucks were killed to a point dangerously near extinction. Following this there was a period of complete protection and finally the present laws which permit open season on bucks but only limited killing of does in certain areas. The net result of these policies has been a gradually increasing population to the point where the coactions upon the winter browse is strikingly evident. It is well known that when deer establish habits of winter feeding in certain areas they are loath to leave such areas and may even become weakened or starved after available browse is utilized rather than move to new areas where food is more available. This same general situation prevails in many parts of the Wasatch chaparral.

The principal plants browsed by the deer in the Wasatch chaparral are the cliff rose *(Cowania stansburiana)* and mountain mahogany *(Cercocarpus ledifolius)*. Antelope bush *(Purshia tridentata)* is also utilized to some extent but is less prevalent in the area studied. In general these shrubs occupy dry ridges or south slopes and grow in a rather open stand. The extent to which the Gambel oak is used as browse is somewhat variable depending upon the availability of more favored foods. In many areas practically no other shrubs are available, and in such places the oaks are browsed extensively to the point where the bushes show marked evidence of alteration.

In any event it must be said that the oak is of great if not principal importance as a cover for deer especially during the daytime period of bedding down. In winter the animals almost invariably seek dense clusters of oak during the daytime, from which they gradually filter out into more favorable feeding areas late in the afternoon. The gray color of the oak at this season corresponds almost exactly with the gray winter coat of the deer and serves to hide them most effectively.

Population studies of the deer have not been undertaken to any extent by the writer. Traveling on foot or even by horse it is impossible to gain anywhere near an accurate estimate of the numbers because of the effective concealment afforded by the chaparral. Airplanes, flown low over an area in early evening or over winter feeding area, appear to the writer to be the only possible approach to this problem. It is impossible to gain an accurate estimate by any means in summer when the animals are scattered and the leaves are on the shrubs.

With the exception of the coyote the large predatory mammals are quite or nearly extirpated from the chaparral. Signs of coyote are common in the community and animals are occasionally seen during field work. The cougar is very rare at the present time and the bobcat is an infrequent inhabitant especially of the more rugged and rocky portions of the community. The badger has been seen on one occasion only in the chaparral, but the earth mounds and dens are frequently encountered especially in the upper portions of the community. The black bear has been observed in the chaparral bordering the montane forest but is a very rare animal in the Wasatch. The wolf and grizzly bear are completely exterminated in this area.

Of the smaller predatory mammals the Nevada weasel is the most common throughout the chaparral community. The tracks are frequently seen in the snow, and the animals themselves are often encountered in field work. Both the spotted skunk and Great Basin skunk occur in the chaparral but both are uncommon at the present time.

Theoretically the larger carnivors at least should be considered as major influents in any community, but their relentless persecution by man has placed them in such a position that they actually are of minor importance ecologically in the present-day activity of the chaparral. The only two species of consequence ecologically are the coyote and the badger, both of which exert considerable control upon the populations of ground squirrels, gophers and to a minor degree upon rabbits.

From the point of view of abundance and ecological interest the Rodentia constitutes a most important group of mammals in the Wasatch chaparral. A list of species known to inhabit the community is given in Appendix B. Nearly all of the rodents are active throughout the entire year, but indications are that the smaller species at least attain their maximum populations in late summer. Mammals which attain complete or partial hibernation include the jumping mouse, marmot, Uinta ground squirrel, mantled ground squirrel, Utah rock squirrel, least chipmunk, and cliff chipmunk. It appears that complete winter dormancy is attained only by the first four listed, all of which are essentially montane species that extend down into the chaparral. In the case of the jumping mouse little direct information is available regarding the beginning and end of hibernation. Of some thirty collection records available from the area studied and contingent communities the latest date is September 9 at which time the animal was very fat, an indication that hibernation may have been near. Specimens have been collected as early as May 3. It appears that the hibernation period of the marmot varies considerably with the elevations, and more is known about its activities at higher elevations than at the level of the chaparral. The writer's own notes place March 20 as the earliest date of appearance in spring, but indications are that the animals are out earlier than this. Marmots may stay out as late as October 1 at 10,000 feet elevation but probably hi-

bernate somewhat earlier at lower levels because of the failure of succulent food. No first hand information is available regarding the hibernation habits of the mantled ground squirrel on account of the scarcity or complete absence of the animal in areas most carefully studied.

The Utah rock squirrel and two species of chipmunk presumably do not enter into true hibernation, but there are periods when, during severe winter weather, they are quiescent for short periods of time. Tracks and indications of feeding activities of all three species are evident in the snow throughout the winter. *Eutamias dorsalis* and *Eutamias minimus* have been collected and observed as early as April 1 at high altitudes in the chaparral when there was still much snow and temperature conditions were below freezing in the daytime.

With regard to the layer society relationships of the chaparral mammals it may be said that there are varying conditions of permeance in common with other communities. The pocket gopher is most nearly confined to flats or floodplains where there is sufficient soil for its burrowing activities. Judging from the number of times this animal is captured by predatory birds and the frequency with which green vegetation is found in the cheek pouches, it is likely that it spends more time on the surface of the ground than is commonly supposed. In the main the mice are associated with the ground and herb layers. They seek hiding places in holes, stumps, or rock crevices but gain most of their food from seeds of herbs which are gleaned from the ground or from the herbaceous vegetation. *Peromyscus maniculatus*, however, climbs freely into shrubs and has been observed by the writer to build its nests in a hollow stump as much as ten feet from the ground.

All of the squirrels and chipmunks of the chaparral with the possible exception of the marmot are permeants in all of the layer societies. *Citellus armatus* is more confined to the ground than any member of the group, since it gains the greater part of the food from succulent forbs. However, this species is frequently seen well up in the shrubs where fruits are available. *Citellus variegatus* not only feeds on acorns and other fruits but often sleeps in a convenient crotch or suns itself on a horizontal limb. Both *Eutamias minimus* and *E. dorsalis* climb actively about in shrubs and obtain part of their food there.

Rabbits in general are associated with the herb layer, but when deep snow prevails at higher elevation in the chaparral they may feed upon the terminal twigs and buds of many of the shrubs. This is particularly true of the snowshoe rabbit *(Lepus bairdi)* that extends into the upper part of the chaparral from the montane forest.

The porcupine *(Erethizon epixanthum)* and flying squirrel *(Glaucomys sabrinus)* are probably most characteristic of the shrub layer, but both of these mammals permeate into the other layers for part of their activities. The porcupine feeds upon the bark of most of the shrubs including the oak, and its coaction in this regard is very apparent in many areas. This animal also frequents caves or large holes where the young are apparently born. The flying squirrel is more likely to inhabit floodplains or other areas where conditions are favorable to the growth of trees or large shrubs where it can find hollow stumps for its nests. During feeding activities, however, this squirrel frequently visits the ground.

Population studies of small mammals at two elevations in the chaparral have been undertaken at several points, and the results are indicated in Tables 12, 13, and 14. These figures were obtained by plot trapping of half acre areas over at least four consecutive nights. While the results of such studies probably do not represent accurately the actual numbers they are of value in a comparative evaluation of the populations. Comparison of figures from plot trapping in climax communities by the author (1945) at several elevational stations on the Wasatch Mountains together with the data obtained by Fautin (1946) using a similar trapping method indicates a generally higher population in the mid altitudes occupied by the chaparral. Data complied from these sources as well as from the present study show the following results in numbers per hectare:

Shadscale, 4,400 feet (Fautin)	42.2
Lower chaparral, 5,500 feet (Table 13)	117.5
Upper chaparral, 6,800 feet (Table 12)	56.5
Lower montane climax, 7,000 feet (Hayward)	30.9
Upper montane climax 10,000 feet (Hayward)	30.4

Data from seral communities of the chaparral indicate, as would be expected, a much higher population of the small rodents in the developing stages. One study of a partly isolated area of an early rocky xerosere in the chaparral indicated as many as 680 mammals per hectare as compared to about 117 in a nearby climax stage (Tables 13, 14).

BIO-ECOLOGICAL AND FAUNISTIC POSITION OF THE WASATCH CHAPARRAL

VEGETATIONAL RELATIONS WITH ADJACENT COMMUNITIES

Certain peculiarities of the Wasatch chaparral make it extremely difficult to classify under the terminology employed by Clements in his several papers and books on plant ecology. In a previous work (1945) the writer considered the Wasatch chaparral as an ecotone between the montane forest above and the northern desert shrub biome (proposed by Fautin 1946) or in many places the pinon-juniper below. This view was based on the fact that the majority of the subdominant plants were characteristically either desert shrub or montane and that few are confined strictly to the climatic zone of the chaparral (Appendix D). Furthermore, the great majority of the vertebrate animals are montane or desert rather than characteristically chaparral.

It should be further pointed out that the community lying between the northern desert shrub or pinon-juniper and the montane forest presents a con-

siderable variation in physiogomy as well as flora even within such a relatively small area as Utah, indicating that minor climatic, edaphic and historic factors have had a great effect upon this community as it lies in a state of rather delicate balance between two major and distinctive climates.

Consideration of several papers on the botany of Utah and adjoining states shows a number of different situations in the dominant vegetation of this mid-community. In the Uinta Basin of northeastern Utah Graham (1937) referred to this community as the sub-montane shrub zone immediately above the pinon-juniper and characterized by Artemisia, Amelanchier, Cercocarpus and other shrubs. The oak (Quercus), so characteristic of the Wasatch chaparral, is almost entirely absent from that region. The yellow pine *(Pinus ponderosa)* is associated with this zone but is not considered as a dominant since it grows in open stands and has little shading influence on the shrubby undergrowth.

Dixon (1935) in her studies of the high plateaus of southern Utah considers the oak chaparral to be a subclimax of the yellow pine climax. Sampson (Tidestrom 1925-28) indicates that in places the oak may replace yellow pine and refers to the community in general as the transition. Daubenmire (1943: 341) refers to the "oak-mountain mahogany zone" as an ecotone and believes that its true position lies in a "broad belt between the juniper-pinon and desert regions in Arizona." However, in Utah, to my knowledge, the chaparral never occupies such a position but lies above the juniper-pinon wherever the two communities are present together (Tanner & Hayward 1934, Behle 1943). Rasmussen (1941) indicates that in the Kaibab forest area of Arizona the oak is not well represented as a distinct belt but mingles more or less with the yellow pine. It occurs, however, above the juniper-pinon. On the east face of the Rocky Mountains (Ramaley 1931) the chaparral is in contact below with the grasslands and above with the yellow pine with which it mingles to a large degree. Clements (1920) in agreement with Daubenmire's statement (1943) states that in areas where the juniper-pinon is below the chaparral, the former is a subclimax which will be ultimately replaced by chaparral. This author believes, therefore, that the normal position of the chaparral is in contact with the grassland below and with the juniper-pinon or montane forest above. Clements (1938) uses the term "petran chaparral" to distinguish the intermountain community from the coastal chaparral.

Daubenmire (1943) points out that the chaparral is typically southern. The oak does not extend north in Utah beyond the southern end of Cache Valley, but chaparral-like communities consisting of mahogany, service berry and other shrubs extend much farther northward.

The interested reader may delve further into the numerous anomalies shown by this community in the intermountain west, but sufficient examples have been given to indicate the complex problems associated with the proper placement of the community in the scheme of bio-ecological classification. In the opinion of the writer, this cannot be accurately done until careful *comparative* bio-ecological studies are made of the different types of chaparral communities represented in the intermountain area.

Insofar as the Wasatch chaparral is concerned certain floristic features are evident and quite characteristic. (1) The community itself, because of the predominance of oak, is strikingly characteristic as to life form and general aspect from adjoining communities. (2) Contact above is with the montane forest from which the yellow pine is absent. (3) Contact below is not with the pinon-juniper, which is absent as a distinct belt, but with the northern desert shrub or grassland. (4) The great majority of the subdominant and some of the dominant plants are not confined to the chaparral but are more characteristic of one or the other of the adjoining communities.

The total absence or scarcity of both the yellow pine and juniper from the Wasatch chaparral is quite difficult to explain from an edaphic point of view since yellow pines introduced at various places appear to do well and junipers do grow in limited numbers. However, their absence or scarcity can possibly be explained when the geological history during and since the Pleistocene is taken into account. Assuming that the oak, yellow pine, and juniper-pinon were all represented in the area previous to the onset of the latest glacial period, either one of two possible climatic changes during the glaciation could have eliminated the yellow pine and pinon-juniper. If the climate were slightly colder and with considerable more precipitation, the more mesophytic oaks and maples could have formed a tree forest which would have effectively dominated the more xeric conifers and crowded them out of existence or at least limited them to dryer ridges. That this is not impossible is indicated by the fact that even today, in favorable places, the oak and maple assume the proportion of small trees.

If, on the other hand, the climate of the glacial period were much colder and dryer, the montane coniferous forest would descend upon the yellow pine and juniper-pinon and dominate them since both are intolerant of shade. The oak, however, being more shade tolerant could survive in favorable places and continue to propagate by vegetative means if no other. One may wonder why, under such a circumstance the yellow pine and pinon-juniper could not retreat to lower elevations. However, it is at once evident that the waters of Lake Bonneville which washed the foot of the Wasatch on the west would preclude any such migration. On the eastern slope the high valleys might have been too cold for the yellow pine and juniper, or else might have supported a grassland which would not permit the invasion of the conifers.

Following the latest period of glaciation the oak-maple forest, if such existed, may have been reduced to a chaparral; or the montane forest might have retreated to higher elevations leaving the chaparral

to take full possession. If the yellow pine were completely obliterated from the Wasatch front, as is supposed by the above theory, its return to the area would be an exceptionally slow process, and its absence at the present time may be accounted for by a lack of time. The juniper, on the other hand could be more readily reestablished through the agency of birds or other means which would explain its scattered nature over most of the Wasatch area at the present time.

Faunal Relationships with Adjoining Communities

The faunal relationship of the chaparral to adjoining communities also shows many ecotonal characters. While the distribution of invertebrates is not too well known, it is evident that the animals associated with the ground and with the subdominant plants are not particularly characteristic of the chaparral but extend into it from the adjoining altitudinal communities. The only group of invertebrates belonging exclusively to the chaparral are the large numbers of parasitic and gall-forming Hymenoptera that appear to be associated with the oak and in many cases dependent upon it for the completion of their life histories. As has been pointed out, neither the taxonomy nor the life histories of most of these species is known. A few other insects, notably the weevil *Balaninus tubulatus*, are known to be intimately associated with the oak and several species of Psyllidae (Pachypsylla) are confined to the hackberry (Celtis).

Distributional relationships of the vertebrates of the chaparral to adjoining communities are indicated in Figures 4, 5, and 6. Since the range of these is better known, the charts can be drawn with greater accuracy. Only the more abundant species are included in the charts and in the case of birds only the nesting population is taken into account. The distribution indicated for the mule deer would hold good only for the year as a whole and would be altered seasonally by migration.

A study of these distributional charts clearly indicates that by far the majority of the species of vertebrates belong essentially either to the montane forest or the desert shrub communities. It is doubtful if one can designate any mammal that is characteristic of the Wasatch chaparral, and certainly there is none entirely confined to it. From the available records it seems that the bobcat, Utah rock squirrel, and cliff chipmunk may reach their greatest populations in this community but neither is by any means confined to it. Possibly the most distinctive feature of the chaparral from the point of view of its mammals is the absence of certain species that are abundant in the desert shrub area. The kangaroo rat (Dipodomys) for example apparently does not extend at all into the chaparral, but this is undoubtedly due to edaphic conditions rather than to circumstances of climate, since there animals require deep sand or at least relatively soft earth in which to burrow, and the steep slope of the Wasatch front is not conducive to such a habitat. The apparent absence or great scarcity of the Piute ground squirrel *(Citellus townsendii mollis)* and white-tailed antelope squirrel *(Citellus leucurus leucurus)* is less easily explained. Pocket mice *(Perognathus)* are also very rare in the chaparral.

The two species of pocket gophers that occur in the Wasatch area (Durant 1946) extend into the chaparral in favorable localities where the soil is of sufficient depth, but the animals are absent over most of the steep hillsides where the soil is too dry and hard in summer for their burrowing activities. On the chaparral flats of the west slope of Mt. Timpanogos, *Thomomys talpoides wasatchensis*, typically a high elevation species extends downward to elevations of about 5,500 feet while the lowland *Thomomys bottae albicaudatus* extends some distance up the canyons along stream courses. It is likely that the ranges of the two species may meet in certain areas of canyons, but in the main the steep slopes and hard-dry soils of the greater part of the Wasatch front serve as effective barriers.

As was pointed out previously in this paper the occurrence of birds in the Wasatch chaparral varies seasonally due to the migratory activities. The conditions indicated in Figure 5 and remarked upon here apply, therefore, only to the breeding season which is the time of greatest population stability. As in the case of mammals the great majority of birds breed in both the chaparral and adjacent communities. The spurred towhee, Virginia warbler, green-tailed towhee, and Woodhouse jay appear to be the most characteristic breeding species and seem to be almost strictly confined to the chaparral in the Wasatch area. Since all of these species are very common summer residents and some remain throughout the year, they accomplish much in support of the idea that the chaparral should be considered as a distinct community and not an ecotone.

The reptilian inhabitants of the chaparral (Fig. 4) set the same general pattern as the mammals and birds in regard to their community affinities. However, it will be noted that the great majority of the species represented belong principally to the desert shrub, but many of them extend well into the chaparral or even through it. The only two species that may be confined mainly to the community, namely, *Charina bottae* and *Hypsiglena o. deserticola*, are not well enough known for definite conclusions to be drawn as yet, but indications are that the former species, at least, may be strictly confined to the upper part of the chaparral. The only characteristically montane forest reptile is the smooth green snake (Opheodrys) which may extend into the upper edge of the chaparral at least during hibernation.

When all of the biotic factors are taken into account it would seem that insofar as the Wasatch chaparral is concerned, certain features indicate that this community should be considered as a distinct biome while others point toward its ecotonal nature. In favor of the biome are:

1. The distinctive life form of the dominant vege-

tation (chaparral) in contrast to the adjoining altitudinal communities.

2. A few characteristic birds and mammals (all minor influents) that appear to be nearly or quite confined to it.

3. A considerable number of invertebrates, mostly parasitic Hymenoptera, that are associated definitely with the oak and other dominant shrubs and give a somewhat exclusive insect fauna to the chaparral.

In opposition to the above features and in favor of the ecotonal concept are the following points:

1. There is a distinct lack of uniformity in the dominant vegetation of the chaparral even within the limits of Utah and the life-form as it appears on the Wasatch front is not distinctive of large contiguous areas.

2. The subdominant vegetation is predominantly a mixture of montane and desert shrub species.

3. No major influent animals are confined to or characteristic of the chaparral.

4. The great majority of the minor influents and subinfluents found in the chaparral belong essentially either to the montane forest or the desert shrub and are not characteristic of the chaparral.

From the point of view of the plant ecologist the distinctive life form of the dominant vegetation would indicate a separate formation (the *Quercus-Ceanothus* formation of Clements). However, when the entire community (plant and animal) is taken into account, and all of the factors mentioned above are carefully weighed it would appear more logical to consider it as an ecotone between the valley shrub (Northern Desert Shrub Biome of Fautin 1946) and the montane part of the Transcontinental-Montane Coniferous Forest Biome proposed by Hayward (1945: 3).

SUCCESSION

Neither plant nor animal succession within the Wasatch chaparral has been studied in any detail, and it is possible at the present time to record only general features. In common with succession in other areas, both hydroseres and xeroseres are in evidence although the latter are far more extensive and important in the communities.

Hydroseres develop almost exclusively from permanent streams in the bottoms of steep-walled canyons, since the steep face of the mountains in most areas excludes the possibility of lakes and ponds. Small seeping springs occasionally give rise to very limited hydroseres, but these waters usually sink into the ground shortly after they arise. Small ravines that may carry a certain amount of water during the spring run-off or summer storms generally have the bottoms washed clean and the effect of the water in this case is not a hydrosere but the beginning of a xerosere on dry ground.

Permanent streams, issuing from canyons into the valleys, give the best example of hydroseres in the chaparral. Provo River is a good and typical example. Most of these streams issue from narrow and steep-walled canyons but in a few cases a flat canyon floor of a hundred yards or more may occur. The vegetation of these canyon floors has been greatly disturbed by man especially by the trailing of livestock to and from the montane summer pastures. There is, therefore, little indication of the successional nature of much of the native vegetation.

The streams themselves are characterized by swift-running waters and rocky bottoms. On account of the diversion of much of this water into irrigation and power canals the nature of the streams have been considerably modified, and the occurrence of a landslide in Provo Canyon in 1930 effectively modified a segment of Provo River in that area. Animal life in the rivers and streams is only now being studied in some detail, but the invertebrates include large populations of stone fly, caddis fly, and May fly larvae as well as numerous Diptera larvae and other species that are able to withstand the swift current or hide under the protection of rocks. The fish fauna of these streams has been greatly modified by the introduction of exotic species and there is little to indicate the precise conditions that occurred previous to the advent of the white man.

Aquatic or land birds closely associated with the streams include several species of ducks, especially buffle-heads and golden eyes that are present in winter. The belted kingfisher gains most of its food directly from the water but is not a common bird. The beaver, muskrat, navigator shrew, mink, and rarely the otter are closely associated with the streams, and the reactions of the beaver in modifying the habitat are becoming considerably more evident as the animals increase in numbers.

Bordering the streams there is typically a narrow floodplain characterized by a type of vegetation strikingly different from the chaparral in general. This vegetation consists of a thicket of several species of willows (Salix), dogwood *(Cornus stolonifera)*, rose (Rosa), hawthorn *(Crataegus rivularis)*, squawbush *(Rhus trilobata)*, birch *(Betula fontinalis)*, alder *(Alnus tenuifolia)*, and a taller tree layer of cottonwood *(Populus angustifolia)*, and boxelder *(Acer interius)*. There is also a herb layer, in the main greatly modified by grazing or other human factors, but composed of a considerable variety of grasses, sedges and forbs.

The invertebrate portion of the matrix of the floodplain stage has not been studied from an ecological point of view, and only general observations can be made upon the vertebrates. Mammalian inhabitants are about the same as those of the climax chaparral, but preliminary studies indicate that the populations are considerably higher in the former. Birds of the floodplain stage include most of the species common to the climax chaparral, but in addition include a number of species that extend upward along the streams from similar streamside communities that occur in the valley. The yellow warbler, mountain song sparrow, fox sparrow, catbird, long-tailed chat, little flycatcher, western warbling vireo, and willow thrush are the more common examples of this group of birds. The sharp-shinned hawk usually nests in this com-

munity but ranges out into the climax to feed, while the other species listed are nearly or quite confined to the floodplain stage.

Floodplain stream borders as well as the streams and adjacent small ponds afford the only habitat in the chaparral where Amphibia are able to live. Two species of toads (*Bufo boreas* and *Bufo woodhousii*) and several frogs (*Pseudacris nigrita triseriata, Rana pipiens*, and *Rana pretiosa pretiosa*) are the most commonly represented species. The wandering garter snake (*Thamnophis ordinoides vagrans*) is more common in the floodplain community but also extends somewhat into the climax chaparral.

Xeroseres develop from two principal conditions: (1) Bare areas on soil caused by floods, land slides, fire or cultivation; and (2) exposed cliffs and rockslides. In addition there are numerous conditions of partial denudation or severe disturbance by the grazing of livestock. Cottam & Evans (1945) have described the effects of grazing on the chaparral in certain areas of the Wasatch, but as far as the writer is aware there has been no over-all study of plant or animal succession in the chaparral community. In keeping with this circumstance, the comments that can be made at this time must be very general and apply mainly to the sere developing from the exposed rock ledges. These ledges or cliffs appear most often on the sides of steep erosional canyons and may rise several hundreds of feet from the canyon floor (Fig. 1). All of these ledges are subject to continuous forces of erosion and are more or less unstable. Slide rocks (talus) at the bottom of these cliffs are in more of a state of flux than the more solid rock masses above.

These unstable stages in the community afford but a precarious foothold for vegetation in general, but a few crevice seed plants are able to grow and on moist northfacing areas mosses form a conspicuous phase of the vegetation. As in the case of other seres, the details of succession in the biotic matrix have not been worked out, but certain observations on the vertebrates may be pointed out.

The True white-footed mice (*Peromyscus truei nevadensis*) appear to be confined entirely to rocky exposures where they are very abundant. They live in rock crevices and are active throughout the entire year. It appears, however, that this species does not range northward much beyond Provo. The life history of this mouse has been studied by Miller (1947). The porcupine (*Erethizon epixanthum*) and bobcat (*Lynx uinta*) both have dens in the numerous caves that are found in this stage. The pallid lump-nosed bat (*Corynorhinus rafinesquii pallescens*) also lives in caverns, oftentimes in large concentrations. Both the Utah rock squirrel (*Citellus variegatus utah*) and Utah cliff chipmunk (*Eutamias dorsalis utahensis*) commonly occur in these rocky habitats but neither is by any means confined to them.

Among the birds there are a number of species that seek the protection of cliffs as nesting sites. The golden eagle, western red-tail, ferruginous rough-leg, prairie falcon, eastern sparrow-hawk, and Montana horned owl build their nests on ledges. The white-throated swift seeks rock crevices, and the cliff swallow builds its mud nests under the protection of overhanging rocks. Ravens also build their nests on rock ledges and the turkey vulture nests in caves. Both the canon wren and the rock wren are characteristic breeding birds of these early stages, and the former species remains throughout the year. Nearly all of these species use the cliffs solely as nesting sites but move freely out into the other stages to feed. However, the canon wren seems to be strictly confined to the rocky areas and the rock wren nearly so.

Another stage in the xerosere is indicated by exposed ridges which represent old rocky exposures that have been well eroded and somewhat stabilized. Here the soil is very shallow and there are numerous rock exposures that are usually well crumbled by the forces of erosion. On such ridges the vegetation assumes a strikingly different aspect. The predominant vegetation here consists of the mountain mahogany (*Cercocarpus ledifolius*) and the cliff rose (*Cowania stansburiana*) with a few scattered junipers (*Juniperus scopulorum*). It is upon these ridges that the mule deer obtains the principal part of its winter browse. The Woodhouse and Stellar jay also nest in this stage.

SUMMARY

The present study is a result of field work carried on in the Wasatch chaparral at intervals over a period of about fifteen years. The work has consisted of both qualitative and quantitative collections, general field observations, and the accumulation of some climatic data.

In the Wasatch Mountains of Utah the chaparral occurs on slopes at medium elevations of 5,100 to 7,500 feet depending upon the slope exposure. It is characterized by thickets of tall shrubs of which the Gambel oak is dominant. The community is in contact above with the lower montane forest and below with the northern desert shrub or grassland communities of the valley. The greater portion of it has been greatly abused and modified by the grazing of livestock.

The position of the chaparral among the biomes of North America as proposed by a number of bioecologists is somewhat peculiar. From the point of view of its dominant plants and general appearance it forms a distinctive and striking formation, but when all of the subdominant plants and the great majority of animals are taken into consideration, it possesses many of the qualities of an ecotone. In the light of these latter considerations it is here considered as an ecotone.

Three rather distinctive layer communities may be recognized in the biotic matrix. The ground layer consists of open areas with low populations of invertebrates where the animals depend for protection upon the shelter of rocks, and shaded areas under the shrubs where there is a much higher population of invertebrates under the protection of several inches

of fallen leaves. Both types of soil communities are subject to season fluctuations in populations of the invertbrate constituents. Mites constitute the most abundant animals under shrubs while ants are very important in open areas.

The herb-low shrub layer consists mainly of grasses, sagebrush, and rabbitbrush in protected areas. It is the layer that has been most affected by overgrazing. Both its plant and animal constituents are essentially either montane or desert, and it has few peculiar characteristics of its own.

The tall shrub layer dominates the community in the climax stage. It is characterized by high populations of invertebrates with many genera of parasitic and gall-forming Hymenoptera very conspicuous. In summer it forms a dense cover for many of the larger animals and exerts a profound influence upon the biotic conditions of the ground beneath it.

Most of the major and minor influent animals of the chaparral extend into it either from the montane forest or desert shrub, or else pass through it as migrants. This community affords an important wintering ground for deer. Subclimax communities of mahogany and cliff rose are favored areas for food, but the oak is also extensively browsed. The Utah rock squirrel and Utah chipmunk are very characteristic of the chaparral but are not confined to it in distribution.

Birds constitute one of the most interesting and important influents of the community. The spurred towhee, green-tailed towhee, Wright flycatcher, Virginia warbler and Woodhouse jay appear to be nearly confined to it during the nesting season. The steep and exposed slopes, usually bare of snow in winter, provide a desirable feeding ground for large numbers of wintering birds.

Succession was not studied in detail but general observations were made on the principal seres. Deep erosional or glaciated canyons often support permanent streams with narrow floodplains of willow and cottonwood. These same canyons also expose extensive cliff areas and other rocky exposures where numerous seral stages are in evidence. The floodplain vegetation in general supports the same animals that inhabit it in the valleys.

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APPENDIX A

Check-list of Birds Known to Inhabit the Wasatch Chaparral. Nomenclature is that of Behle: Check-list of the Birds of Utah, Condor **46:** pp. 67-86, 1944. PR = Permanent Resident; WV = Winter Visitant; SR = Summer Resident; MT = Migrant or Local Transient.

Ardea herodias treganzai Court Treganza Blue Heron	MT
Nycticorax nycticorax hoactli (Gmelin) Black-crowned night Heron	MT
Anas platyrhynchos platyrhynchos L. Mallard	MT
Bucephala albeola (L.) Buffle-head	MT
Bucephala clangula americana (Bonaparte) American Golden-eye	MT
Anas acuta tzitzihoa Vieillot Pintail	MT
Cathartes aura teter Friedmann Western Turkey Vulture	SR
Accipiter gentilis atricapillus (Wilson) Eastern Goshawk	PR
Accipiter striatus velox (Wilson) Sharp-shinned Hawk	PR
Accipiter cooperii (Bonaparte) Cooper Hawk	SR
Buteo jamaicensis calurus Cassin Western Red-Tailed Hawk	PR
Buteo swainsoni Bonaparte Swainson Hawk	MT
Buteo regalis (G. R. Gray) Ferruginous Rough-legged Hawk	SR
Aquila chrysaëtos canadensis (L.) Golden Eagle	PR
Circus cyaneus hudsonius (L.) Marsh Hawk	MT
Falco mexicanus Schlegel Prairie Falcon	SR
Falco sparverius sparverius L. Eastern Sparrow Hawk	SR
Dendragapus obscurus obscurus (Say) Dusky Grouse	PR
Bonasa umbellus incanus Aldrich & Friedmann Hoary Ruffed Grouse	PR
Lophortyx californica (Shaw) California Quail	PR
Phasianus colchicus torquatus Gmelin Ring-necked Pheasant	PR
Actitis macularia (L.) Spotted Sandpiper	SR
Larus californicus Lawrence California Gull	MT
Zenaidura macroura marginella (Woodhouse) Western Mourning Dove	SR
Otus asio inyoensis Grinnell Inyo Screech Owl	PR
Bubo virginianus occidentalis Stone Montana Horned Owl	PR
Asio otus wilsonianus (Lesson) Long-eared Owl	PR
Chordeiles minor hesperis Grinnell Pacific Nighthawk	SR
Phalaenoptilus nuttallii nuttallii (Audubon) Nuttall Poorwill	SR
Aëronautes saxatalis saxatalis (Woodhouse) Western White-throated Swift	SR
Archilochus alexandri (Bourcier and Mulsant) Black-chinned Hummingbird	SR
Selasphorus platycercus platycercus (Swainson) Broad-tailed Hummingbird	SR
Selasphorus rufus (Gmelin) Rufous Hummingbird	MT
Megaceryle alcyon caurina (Grinnell) Western Belted Kingfisher	SR
Colaptes cafer collaris Vigors Red-shafted Flicker	PR
Asyndesmus lewis Gray Lewis Woodpecker	MT
Sphyrapicus varius nuchalis Baird Red-naped Sapsucker	MT
Dryobates pubescens leucurus (Hartlaub) Rocky Mountain Downy Woodpecker	PR
Empidonax traillii brewsteri Oberholser Little Flycatcher	SR
Empidonax oberholseri Phillips (= wrightii Baird) Wright Flycatcher	SR
Empidonax hammondii (Xantus) Hammond Flycatcher	MT
Myiochanes richardsonii richardsonii (Swainson) Western Wood Pewee	SR
Nuttallornis borealis borealis (Swainson) Olive-sided Flycatcher	MT
Tachycineta thalassina lepida Mearns Violet-green Swallow	MT
Iridoprocne bicolor (Vieillot) Tree Swallow	MT
Riparia riparia riparia (L.) Bank Swallow	SR
Pterochelidon albifrons hypopolia Oberholser Cliff Swallow	SR
Cyanocitta stelleri ssp. Steller Jay	PR
Aphelocoma californica woodhouseii (Baird) Woodhouse Jay	PR
Pica pica hudsonia (Sabine) American Magpie	PR
Corvus corax sinuatus Wagler American Raven	PR
Corvus brachyrhynchos hesperis Ridgway Western Crow	WV

Cyanocephalus cyanocephalus (Wied)
Pinyon Jay MT
Nucifraga columbiana (Wilson)
Clark Nutcracker MT
Parus atricapillus nevadensis (Lindsdale)
Nevada Black-capped Chickadee PR
Parus gambeli gambeli Ridgway
Mountain Chickadee WV
Parus inornatus ridgwayi Richmond
Gray Titmouse MT
Psaltriparus minimus plumbeus (Baird)
Lead-colored Bush-tit MT
Certhia familiaris montana Ridgway
Rocky Mountain Creeper WV
Troglodytes aedon parkmanii Audubon
Western House Wren SR
Nannus hiemalis pacificus (Baird)
Western Winter Wren WV
Catherpes mexicanus conspersus Ridgway
Canyon Wren PR
Salpinctes obsoletus obsoletus (Say)
Rock Wren SR
Dumetella carolinensis (L.)
Catbird SR
Oreoscoptes montanus (Townsend)
Sage Thrasher MT
Turdus migratorius propinquus Ridgway
Western Robin PR
Hylocichla guttata auduboni (Baird)
Audubon Hermit Thrush SR
Hylocichla fuscescens salicicola Ridgway
Willow Thrush SR
Sialia currucoides (Bechstein)
Mountain Bluebird SR
Myadestes townsendi (Audubon)
Townsend Solitaire WV
Polioptila caerulea amoenissima Grinnell
Western Gnatcatcher MT
Regulus regulus olivaceus Baird
Western Golden-crowned Kinglet WV
Regulus calendula cineraceus Grinnell
Western Ruby-crowned Kinglet WV
Bombycilla garrula pallidiceps Reichenow
Bohemian Waxwing WV
Bombycilla cedrorum Vieillot
Cedar Waxwing WV
Vireo gilvus leucopolius Oberholser
Oregon Warbling Vireo SR
Vermivora celata orestera Oberholser
Rocky Mountain Orange-crowned Warbler MT
Vermivora ruficapilla ridgwayi van Rossem
Calaveras Warbler MT
Vermivora virginiae (Baird)
Virginia Warbler SR
Dendroica aestiva morcomi Coale
Rocky Mountain Yellow Warbler SR
Dendroica auduboni auduboni (Townsend)
Northern Audubon Warbler MT
Dendroica auduboni memorabilis Oberholser
Rocky Mountain Audubon Warbler MT
Oporornis tolmiei (Townsend)
Macgillivray Warbler SR
Icteria virens auricollis Bonaparte
Long-tailed Chat SR
Wilsonia pusilla pileolata (Pallas)
Northern Pileolated Warbler MT
Sturnella neglecta Audubon
Western Meadowlark PR
Euphagus cyanocephalus cyanocephalus (Wagler)
Brewer Blackbird MT
Piranga ludoviciana (Wilson)
Western Tanager MT
Hedymeles melanocephalus melanocephalus (Swainson)
Rocky Mountain Black-headed Grosbeak SR
Passerina amoena (Say)
Lazuli Bunting SR
Hesperiphona vespertina brooksi Grinnell
Western Evening Grosbeak WV
Carpodacus mexicanus (Say)
House Finch PR
Pinicola enucleator montana Ridgway
Rocky Mountain Pine Grosbeak WV
Leucosticte tephrocotis littoralis Baird
Hepburn Rosy Finch WV
Leucosticte tephrocotis tephrocotis (Swainson)
Gray-crowned Rosy Finch WV
Leucosticte atrata Ridgway
Black Rosy Finch WV
Spinus pinus pinus (Wilson)
Northern Pine Siskin PR
Spinus tristis pallidus Mearns
Pale Goldfinch PR
Oberholseria chlorura (Audubon)
Green-tailed Towhee SR
Pipilo maculatus montanus Swarth
Spurred Towhee PR
Pooecetes gramineus confinis Baird
Western Vesper Sparrow MT
Junco hyemalis hyemalis (L.)
Slate-colored Junco WV
Junco oreganus montanus Ridgway
Montana Junco WV
Junco oreganus mearnsi Ridgway
Pink-sided Junco WV
Junco caniceps caniceps (Woodhouse)
Gray-headed Junco WV
Spizella passerina arizonae Coues
Western Chipping Sparrow SR
Spizella breweri breweri Cassin
Brewer Sparrow MT
Zonotrichia leucophrys oriantha Oberholser
Oregon White-crowned Sparrow WV
Zonotrichia leucophrys gambelii (Nuttall)
Gambel Sparrow WV
Passerella iliaca schistacea Baird
Slate-colored Fox Sparrow SR
Melospiza melodia montana Henshaw
Mountain Song Sparrow PR

APPENDIX B

Check-list of Mammals Known to Inhabit the Wasatch Chaparral.

Sorex vagrans monticola (Merriam)
Mountain Shrew
Corynorhinus rafinesquii pallescens Miller
Pallid Lump-nosed Bat
Mustela frenata nevadensis Hall
Nevada Weasel
Mustela vison energumenos (Bangs)
Western Mink
Spilogale gracilis saxatilis (Merriam)
Great Basin Spotted Skunk
Mephitis occidentalis major (Howell)
Great Basin Striped Skunk
Taxidea taxus ssp.
Badger
Canis latrans lestes Merriam
Great Basin Coyote
Felis oregonensis hippolestes (Merriam)
Rocky Mountain Cougar
Lynx uinta Merriam
Mountain Bobcat
Marmota flaviventris nosophora Howell
Golden Mantled Marmot
Citellus variegatus utah Merriam
Utah Rock Squirrel
Citellus lateralis castanurus (Merriam)
Wasatch Mantled Ground Squirrel
Citellus armatus (Kennicott)
Uinta Ground Squirrel

Eutamias minimums consobrinus (Allen)
Wasatch Chipmunk
Eutamias dorsalis utahensis Merriam
Utah Cliff Chipmunk
Tamiasciurus hudsonicus ventorum (Allen)
Wind River Mt. Red Squirrel
Glaucomys sabrinus lucifugus Hall
Utah Flying Squirrel
Thomomys talpoides wasatchensis Durrant
Wasatch Pocket Gopher
Perognathus parvus olivaceus (Merriam)
Great Basin Pocket Mouse
Castor canadensis ssp.
Beaver
Reithrodontomys megalotis megalotis (Baird)
Desert Harvest Mouse
Peromyscus maniculatus ssp.
White-footed Mouse
Peromyscus truei nevadensis Hall and Hoffmeister
Pinyon Mouse
Peromyscus boylii utahensis Durrant
Utah White-footed Mouse
Neotoma cinerea acraia (Elliott)
Bushy-tailed Wood Rat
Clethrionomys gapperi galei (Merriam)
Gale Red-backed Mouse
Microtus longicaudatus mordax (Merriam)
Long-tailed Meadow Mouse
Lemmiscus (= Lagurus) *curtatus* ssp.
Sagebrush Vole
Ondatra zibethica osoyoosensis (Lord)
Rocky Mt. Muskrat
Zapus princeps utahensis Hall
Utah Jumping Mouse
Erethizon epixanthum epixanthum Brandt
Yellow-haired Porcupine
Lepus bairdi bairdi Hayden
Rocky Mt. Snowshoe Rabbit
Lepus californicus deserticola (Mearns)
Desert Jackrabbit
Lepus townsendii townsendii Bachman
Western White-tailed Jackrabbit
Sylvilagus nuttalli grangeri (Allen)
Black Hills Cottontail
Cervus canadensis canadensis (Erxleben)
American Wapiti
Odocoileus hemionus macrotis (True)
Mule Deer

APPENDIX C

Check-list of Invertebrates Found in Wasatch Chaparral and Identified to Genus. G = Ground, H = Herb, S = Shrub. Extreme Dates of Collections Are Given. Sta. 2 = Upper Chaparral, Sta. 7 = Lower Chaparral.

	Layer	Sta.	Date
MOLLUSCA (Land species)*			
Helicidae			
Microphysula ingersolli (Bland.)	G	2	
Oreohelix strigosa depressa (Cook)	G	2,7	6-8
Zonitidae			
Vitrina alaskana Dall	G	2	
Euconulus fulvus alaskensis (Pilsbry)	G	2	
Zonitoides arborea (Say)	G	2	
Limacidae			
Agriolimax campestris (Binney)	G	2	
Valloniidae			
Vallonia albula Sterki	G	2	
Pupillidae			
Vertigo modesta corpulenta (Morse)	G	2	
DIPLOPODA			
Taiulus tiganus (Chamberlin)	G	7	5-26 6-6

*Molluscs are not common in the chaparral. Most of the data for this list were supplied through the kindness of Mr. Harry P. Chandler. Dates of collection were not available.

APPENDIX C (Continued)

	Layer	Sta.	Date
CHILOPODA			
Lithobiidae			
Pokabius utahensis (Chamberlin)	G	2	7-5
Schendyla nemorensis (C. Koch)	G	7	5-18
Pokabius socius (Chamberlin)	G	7	7-22
Bothropolys permudus Chamberlin	G	7	6-8
Scolopendridae			
Scolopendra polymorpha Wood	G	7	5-5 6-8
Henicopidae			
Yobius haywardi Chamberlin	G	7	7-12
Chilenophilidae			
Gnathomerium xenoporus (Chamberlin)	G	7	5-5 5-12
ISOPODA			
Porcellionidae			
Porcellionides pruinosus (Brandt)	G	7	5-22
ACARINA			
Ceratozetidae			
Tectoribates sp.	G	7	7-24
Padoribates sp.	G	7	7-3 7-24
Tegeocranidae			
Cepheus sp.	G	7	7-24
Parasitidae			
Gamarellus sp.	G	7	5-12
Laelaptidae			
Seiulus sp.	G	7	5-12
Ascaidae			
Zercon sp.	G	7	5-26 6-6
Galumnidae			
Galumna sp.	G	7	7-3 8-9
Damaeidae			
Gymnodameus sp.	G	7	7-3 7-24
Belba sp.	G	7	7-24
Dameosomidae			
Oppia sp.	G	7	7-24
Caeculidae			
Caeculus	G	7	7-3
Orbatulidae			
Oribatula minuta (Ewing)	G	7	6-6
CHELONETHIDA			
Chthonidae			
Chthonius (Neochthonius) sp.	G	7	5-26 7-24
ARANEIDA			
Vejovidae			
Vejovis borealis W.	G	7	6-8
Vejovis boreus (Girard)	G	7	6-20
Dictynidae			
Titanoeca americana Emerton	G	7	5-26
Dictyna completa C. & G.	S	7	5-26
Hahniidae			
Neoantistea gosiuta Gertsch	G	2	7-5
Hahnia sp.	G	2	7-6
Lycosidae			
Tarentula kochi Keys.	G	2	7-5
Trochosa gosiuta (Chamberlin)	G	7	5-12 6-8
Schizocosa wasatchensis (C. & I.)	G	7,2	5-22 6-8
Pardosa yavapa Chamberlin	G	2	6-2
Theridiidae			
Lactrodectus mactans	G	7	6-20
Euryopis emertoni Bryant	G	7	6-20
Erigonidae			
Ceraticelus lactabilis (Cambridge)	G	7	7-3
Epieridae			
Aranea displicata Hentz	S	2	7-6
Araniella displicata octopunctata (C. & I.)	S	7	7-12
Aranea sp.	H	2	7-27

APPENDIX C (Continued)

	Layer	Sta.	Date
Thomisidae			
Misumenops delphinus Walckenaer	S	7	5-11
Misumenops lepidus Thorell	H	2	8-15
Misumenops sp.	H	2	9-10
Xysticus gosiutus Gertsch	S	2	6-11
		7	6-20
Philodromus sp.	S	2	7-27
Tibellus chamberlini Gertsch	H	7	7-24
			8-9
			8-16
			8-10
Misumenops uteanus Gertsch	S	7	5-18
			8-10
Misumenops californicus (Banks)	H,S	7	6-6
Philodromus infuscatus (Keys)	S	7	8-10
Gnaphosidae			
Herpyllus sp.	G	7	5-12
Zelotes sp.	G	7	5-18
Gnaphosa muscorum C. Koch	G	2	6-2
Drassodes neglectus (Keys)	G	2	6-2
Drassyllus improvisus Chamberlin	G	2	6-2
Drassyllus apachus Chamberlin	G	7	7-12
Clubionidae			
Anyphaena californica (Banks)	S	7	7-7
Phrurotimpus woodburyi C. & G.	G	7	6-26
Cheiracanthium inclusum (Hentz)	H	7	9-4
Salticidae			
Icius similis Banks	H,S	2	6-11
			6-27
Metaphidippus sp.	H	2	7-27
Phidippus sp.	H	2	7-27
Metaphidippus montanus Emerton	S,H	2	5-11
		7	7-20
Evarcha hoyi (Peckham)	S	2	7-5
Metaphidippus verecundus (C. & G.)	G,S	7	5-5
		7	7-7
Paraphidippus marginatus (Walckenaer)		7	7-12
Habronattus brunneus (Peckh.)	H	7	7-14
Sassacus papenhuoi Peckh.	H	7	7-14
Mimetidae			
Mimetus hesperus (Chamberlin)	S	7	8-16
Oxyopidae			
Oxyopes rufipes Banks	H	7	5-12
			8-1[illegible]
ORTHOPTERA			
Locustidae			
Hippiscus griseus Scudder	G,H	2	6-3
			6-14
Arphia simplex Scudder	G,H	2,7	5-26
			6-6
Arphia frigida Scudder	G,H	2	7-6
Hippiscus corallipes (Haldeman)	G,H	7	6-20
Melanoplus m. mexicanus Sauss	G,H	7	6-20
			9-21
Mermeria bivittata Serv.	G,H	7	6-8
			9-7
Hesperotettix viridis Thom.	G,H	7	8-9
			9-21
Trimerotropis cyaneipennis Bruner	G,H	7	8-16
Schistocerca shoshone (Thomas)	G,H	7	9-7
			9-21
Circotettix undulatus Thomas	G,H	7	7-3
			9-21
Tettigonidae			
Scudderia sp.	G,H	7	8-16
Gryllidae			
Oecanthus sp.	S	7	9-4
Oecanthus niveus (DeGeer)	H	7	8-10
ODONATA			
Libellulidae			
Sympetrum semicinctum Say	H,S		7-20-45
NEUROPTERA			
Chrysopidae			
Chrysopa californica Cog.	H	2	7-27-40

APPENDIX C (Continued)

	Layer	Sta.	Date
HOMOPTERA			
Cicadellidae			
Empoasca aspersa (group)	H	2	8-15-39
Phlepsius cumulatus O. & B.	H	2	9-10-40
Dikraneura carneola (Stal.)	H,S	2	5-11
	H	2	8-16
Porabolocratus viridis (Uhl.)	H	7	6-6
			8-16
Psammotettix striatus (L.)	H	7	6-6
	H	7	9-21
Deltocephalus dorsti Oman	H	7	6-6
			8-10
Aceratagallia curvata Oman	H	7	7-7
			9-21
Ophiola sp. (near *vara* Ball)	H	7	7-7
			7-24
Stragania rufoscutellatus (Baker)	H	7	7-14
			7-24
Laevicephalus collinus (Boheman)	H	7	6-20
			9-14
Empoasca neaspersa Oman & Wheeler	H	7	7-14
			8-9
Ballana atridorsum (Van D.)	H	7	7-14
			8-10
Macrosteles wilburi Dorst	H	7	7-24
Empoasca carsona De L. and Dav.	H	7	8-16
Gypona vexana De L.	H	7	9-7
	H	7	9-21
Xerophloea viridis (F.)	H	7	9-14
Laevicephalus abdominalis (F.)	H,S	7	6-20
			7-20
Thamnotettix geminatus Van D.	S	7	5-26-44
			9-7
Aligia curtipennis Hepner	S	7	8-9
Aligia jacunda (Uhl.)	S	7	8-16
Typhlocyba flavomarginata G. & B.	S	7	8-16
			9-7
Erythroneura sp.	S	7	8-16
Colladonus flavocapitatus (Van D.)	S	7	9-7
Deltocephalus grex Oman	H,S	7	6-8
			9-4
Eutettix latus Hapner	H,S	7	7-12
Osbornellus borealis De L. & M.	S	7	9-4
Membracidae			
Cyrtolobus acutus Van D.	H,S	7,2	7-5
			9-7
Strictocephala pacifica Van D.	H	2	7-27
Publilia modesta (Uhl.)	H,S	7	5-18
			9-21
Strictocephala franciscara (Stal.)	H,S	7	9-21
Telamonanthe pulchella (Ball)	S	7	8-9
Kinnaridae			
Oeclidus brickellus Ball	H	7	9-21
Issidae			
Fitchiella rufipes Lawson	H	7	6-6
			9-21
Cixiidae			
Oecleus obtusus Ball	H,S	7	7-14
Oliarus conconinus Ball	H	7	7-20
			8-9
Colladonus flavocapitatus (Van D.)	S	7	7-14
Delphacidae			
Laccocera obesa Van D.	H	7	6-6
			6-20
Stobaera tricarinata (Say)	H	7	9-7
Delphacodes consimilis (Van D.)	H	7	6-20
Dictyophoridae			
Scolops robustus Ball	H	7	7-7
			9-21
Cercopidae			
Aphrophora permutata Uhler	H	7	9-21
Chermidae			
Trioza sp.	H	2	9-10
Trioza frontalis Crawf.	H,S	2	7-5
			7-27-4[illegible]

APPENDIX C (Continued)

	Layer	Sta.	Date
Trioza minuta Crawf.	S	7	6-6
Psylla negundinis Mally	S	2	8-15
Psylla omani Tuth.	S	7	9-14
Aphalara caudata Crawf.	H	7	5-26
Aphalara anomola Crawf.	H	7	6-26
			8-16
Aphalara angustipennis Crawf.	H,S	7	8-16-44
Pachypsylla celtidis-mamma Riley	H,S	7	5-5
			6-8
Aphalara loca Cald.?	S	7	6-6
Psylla americana Crawf.	S	7	7-7
Psylla brivistigmata Patch	S	7	9-7
Pachypsylla celtidis-vesicula Crawf.	H,S	7	5-11
Pachypsylla celtidis-gemma Riley	H,S	7	6-8
Aphidae			
Capitophorus gregarius K.	H	7	7-12
Periphyllus negundinis Thomas	S	7	5-26
Myzocallis alhambra Davidson	S	7	5-22
Macrosiphon pisi (Kalt)	S,H	7	6-8
HEMIPTERA			
Nabidae			
Nabis alternatus Parsh.	S,H	2	6-11
			6-26
Tingididae			
Corythucha sp.	H,S	7	5-26
			8-9
Anthocoridae			
Anthocoris antevolens White	H	2	7-5
Pentatomidae			
Chlorochroa congrua Uhler	H	2	7-27
Euschistus variolarius (P. B.)	G	7	5-5
Euschistus inflatus Van D.	H	7	7-24
Carpocoris remotus Horv.	H	7	8-16
Thyanta custator (Fabr.)	H	7	9-21
Thyanta accerra McAtee	H	7	9-21
Acrosternum hilaris (Say)	S	7	9-21
Homaemus aeneifrons (Say)	H	7	7-20
Miridae			
Lygus desertus Kngt.	H	7	5-5-44
Irbisia brachycerus (Uhl.)	H	7	5-26
			6-20
Psallus sp.	S	7	8-16
Lygaeidae			
Lygaeus pyrrhopterus Stal	G	7	5-26
Nysius ericae (Schill.)	H	7	9-21
COLEOPTERA			
Carabidae			
Discoderus amoenus Lec.	G	2,7	5-5
			7-24
Meloidae			
Pyrota mylabrina Chev.	H	7	9-4
Epicauta ferruginea (Say)	H	7	9-4
Histeridae			
Canthon corvinus Harold	G	2	6-3
Tenebrionidae			
Iphthimus sublaevis Bland	G	2	5-18
Coniontis uteana Csy.	G	7	6-8
Cantharidae			
Silis difficilis Lec.	H	7	5-12
Chauliognathus basalis Lec.	H	7	9-4
Curculionidae			
Cercopeus artimisiae Pierce	H	7	5-12-45
Apion porosicolle Gemm.	H	7	5-12-45
Brachyrhinus ovatus (L.)	G	2	8-15
			6-11
Thricolepis inornata Horn	H,S	2,7	5-26
			7-5
Phyllotrox nubifer Lec.	S	2	6-4
Rhynchites cyanellus Lec.	S	2	6-4
Anthonomus canus Lec.	H	7	5-12
Baris nephiana Csy.	H	7	7-7
Chrysomelidae			
Monoxia sp.	H	2	9-10

APPENDIX C (Continued)

	Layer	Sta.	Date
Luperodes lecontei Cr.	H	2	7-6
Brachycoryna sp.	H	2	7-6
Glyptina sp.	H	2	7-6
Haltica torquata Lec.	S	2	6-14
Galeruca externa Say	G	7	6-8
Systena sp.	H	7	7-12
Phyllotreta sp.	H	7	7-12
Cleridae			
Hydnocera lecontei Wolc.	H	2	6-11
Buprestidae			
Agrilus sp.	H	2	6-11
Acmaeodera variegata Lec.	H	7	6-6
Mordellidae			
Mordella albosuturalis Lilj.	H	2	7-5
Scarabaeidae			
Dichelonyx mormona Fall	S	2	6-11
Dichelonyx truncata Lec.	H	7	6-8
Coccinellidae			
Coccinella quinquemata Kby.	H	7	7-24
Hyperaspis wellmani Nun.	S	7	8-16
Hyperaspis flammula Nun.	S	7	8-16
Hippodamia convergens Guer.	S	2	7-27
Adalia bipunctata L.	S	7	5-5
Cycloneda polita Csy.	H	7	6-8
Anatis lecontei Csy.	S	8	5-26
Adalia humeralis (Say)	S	7	7-20
Melynidae			
Listrus sp.	H	7	7-14
Anthicidae			
Anthicus sp.	H,S	7	6-6
			7-14
Cerambycidae			
Batyle ignicollis (Say)	H	7	7-14
			7-20
Melyridae			
Attalus futilis Fall	S	7	6-20
Eudasytes grandicollis Blais.	H	7	6-26
			7-3
Trichochrous sp.	S	7	7-12
Phalacridae			
Olibrus sp.	S	7	7-14
Dermestidae			
Cryptorhopalum bakeri Csy.	S	7	6-26
			7-20
ICHNEUMONOIDEA			
Ichneumonidae			
Gambrus burkei Vier.	H	2	6-11
Oleiscampe sp.	H	2	6-11
Phytodietus sp.	S	2	6-4
Phaeogenes n. sp.	S	7	5-22
Campoletis patsuiketorum (Vier.)	H	7	6-8
Ophion n. sp.	G	7	6-8
Pterocormus sp.	H	7	6-26
Braconidae			
Microbracon sp.	H	2	5-11
	H	7	6-11
Microbracon auripes (Prov.)	H	2	7-27
Microbracon melanaspis (Ashm.)	H	2	7-27
Gnamptodon n. sp.	S	2	7-5
Microtonus eleodis Vier.	S	7	5-26
Orgilus sp.	H	2	7-5
Apanteles aristoteliae Vier.	S	2	7-27
Apanteles sp.	S	7	7-7
	S	7	8-9
	H	7	9-21
Apanteles ornigis Weed	S	7	8-16
Vipionidae			
Mirax aspidiscae Ashm.	S	7	7-7
CHALCIDOIDEA			
Callimomidae			
Callimome (several sp.)	H,S	2,7	5-12
			9-21
Monodontomerus dianthidii Gah.	S	2	6-11

APPENDIX C (Continued)

	Layer	Sta.	Date
Haltichella	H	7	6-8
Ormyrus sp.	S	7	6-6
	S	7	9-21
Pseuderimerus femoratus Gahan	H	7	8-9
	H	7	8-16
Callimome warreni Ckll. (bred)	S	7	
Callimome rubenidis Huber (bred)	S	7	
Callimome maculipenne (Cam.) (bred)	S	7	
Chalcididae			
Spilochelcis sp.	H,S	7	9-21
Eurytomidae			
Decatoma (several species)	S	2	6-11
			7-5
Eurytoma (several species)	S,H	2	6-6
			9-21
Harmolita (several species)	S	7	5-11-44
			6-6-44
Harmolita grandis (Riley)	S	7	6-20
Eudecatoma sp.	H	7	5-26
Eucharidea			
Halticoptera sp.	H,S	7	5-2^7
			7-1^4
Cleonymidae			
Euchrysia sp.	S	2	7-27
Encyrtidae			
Eupelmus sp.	H,S	7	7-14
			9-21
Calosota metallica Gahan	H	7	8-9
Psyllaephagus pachypsyllae (How.) (bred)	S	7	
Eupelmus allynii (French) (bred)	S	7	
Copidosoma sp.	S	7	6-26
	S	7	7-20
Pteromalidae			
Heteroschema rugosopunctata (Ashm)	S	7	6-6
			7-7
Derostenus sp.	S	7	6-20
			7-14
Habrocytus sp.	H,S	7	6-20
			6-26
Merisus sp.	H,S	7	7-7
			9-21
Amblymerus mayetiolae (Gahan)	H,S	7	5-22
			7-7
Amblymerus sp.	H	7	7-14
			8-16
Merisus atriscapus Gahan	H	7	9-21
Syntomopus sp.	S	7	7-20
Eulophidae			
Pleurotropis sp.	H,S	2,7	6-20
			7-5
Tetrastichus (many species)	H,S	2,7	5-18
			9-21
Elachertus sp.	S	2	7-27
Cirrospilus coptodiscae Gir.	S	2	6-4
Horismenus sp.	S	7	6-20
Aprostocetus sp.	H	7	7-7
Rhicnopeltoidea amsterdamensis Girault	S	7	9-7
Euderus sp.	H	7	6-26
CYNIPOIDEA			
Cynipidae			
Ceroptres (several species)	S	2,7	5-26
			8-15
Rhodites sp.	H	2	6-11
Andricus sp.	S	7	6-6
			6-20
Sarothrus sp.	S	2	7-5
Neuroterus (several species)	H,S	2,7	5-5
			6-6
Synergus sp.	S	2,7	7-7
			7-27
Dryocosmus sp.	S	7	6-6
Bassettia sp.	S	7	5-26
	H	7	5-11

APPENDIX C (Continued)

	Layer	Sta.	Date
Trigonaspis pumiliventris (Boss.)	G	7	6-20
Kleidotoma sp.	H	7	6-20
Trigonaspis fumosa Weld	S	7	7-7
			7-14
SERPHOIDEA			
Platygasteridae			
Amblyaspis sp.	S	7	6-20-44
Platygaster coloradensis Ashm.	H,S	7	5-11
			6-20
Acerota sp.	H	7	6-20
Platygaster sp.	H	7	6-20
Inostemma sp.	H,S	7	7-7
			8-16
Scelio sp.	H	7	7-7-44
Ceraphronidae			
Calliceris (= Ceraphron)	G,S	2,7	7-3
			8-15
BETHYLOIDEA			
Bethylidae			
Pseudisobrachium sp.	H	7	8-10
Dryinidae			
Alphelopus n. sp.	S	2,7	6-11
			6-20
Gonatopus sp.	S	7	7-14
FORMICOIDEA			
Formicidae			
Lasius niger Linn.	H,S	2	6-11
			7-5
Lasius latipes (Walsh)	G	2	6-3
Formica fusca Linn.	G,S	2,7	6-6
			7-5
Formica sp. (rufa group)	S	2	6-11
Tapinoma sessile (Say)	G,H	2,7	6-13
			9-21
Formica neogagates lasioides E.	H,G	2	6-3
			7-27
Monomorium minimum (Buck.)	S,H,G	7	5-11
			9-21
Camponotus maculatus vicinus Mayr.	S	2	9-10
Pheidole sp.	G,H,S	7	5-5
			9-21
Dorymyrex sp.			
Leptothorax nitens Emery	G	7	5-26
Solenopsis molesta validiuscula Em.	G	7	6-6
			7-24
Crematogaster lineolata (Say)	H,S	7	7-14
			9-7
Aphaenogaster uinta Wheeler	G	7	7-24
SPHECOIDEA			
Sphecidae			
Stigmus inordinatus Fox	S	2	8-15
Xylocelia argentinae (Roh.)	H	2	7-6
Tachytes elongatus Cress.	S	7	8-9
VESPOIDEA			
Vespidae			
Eumenes coloradensis Cress.	S	2	7-5
			7-27
Vespula arenaria Fab.	H	2	7-5
Vespula rufa sladeni (Beq.)	S	2	7-27
Vespula rufa atropilosa Sl.	S	7	6-26
Polistes fuscatus utahensis Hayw.	S	2	7-27
	G	7	6-8
Vespula maculata (Linn.)	S	2	7-27
Mischocyttarus flavitarsis idahoensis Beq.	H	7	8-9
Psammocharidae			
Pepsis sp.	H	7	8-9
APOIDEA			
Bremus occidentalis (Greene)	S	2	7-27
Bremus appositus Cress.	S	2	7-27
	H	7	7-20
Bremus bifarius (Cress.)	H	2	7-27
Bremus nevadensis (Cress.)	H	7	5-15

APPENDIX D

List of the More Common Plants of the Wasatch Chaparral. Distributional Groupings Based upon Tidestrom (1925) and Personal Observation.

Confined to Chaparral:

Quercus gambelii Nutt.
Quercus utahensis (A. DC.)
Cercocarpus ledifolius Nutt.

Present in desert shrub and grassland of the valleys and often extending through the chaparral into the lower montane forest:

Mertensia brevistyla S. Wats.
Cercocarpus montanus Raf.
Cowania stansburiana Torr.
Pentstemon cyananthus Hook.
Gutierrezia sp.
Chrysothamnus graveolens (Nutt.) Greene
Artemisia tridentata Nutt.
Cymopterus longipes S. Wats.
Zygadenus paniculatus S. Wats.
Lithospermum ruderale Dougl.
Lappula coerulescens Rydb.
Allium acuminatum Hook.
Astragalus cibarius Sheld.
Astragalus beckwithii Torr. & Gray
Astragalus utahensis Torr. & Gray
Asclepiadora decumbens (Nutt.)
Phlox douglasii Hook.
Zauschneria garrettii A. Nels.
Galium vaillantii DC & Lam.
Erigeron divergens Torr. & Gray
Phacelia linearis (Pursh)
Lygodesmia grandiflora (Nutt.) Torr. & Gray
Petradoria pumila Greene
Astragalus utahensis Torr. & Gray
Pachylophus hirsutus Rydb.
Claytonia rubra (Howell)
Lathyrus utahensis Jones
Lathyrus eucosmos Butters (possibly confined to chaparral)
Agropyron spicatum (Pursh) (Palouse Prairie)
Bromus carinatus Hook and Arn.
Poa secunda Presl. (Palouse Prairie)
Poa longiligula Scribn. & Will.
Poa pratensis L.
Bromus tectorum L.
Oryzopsis humenoides (Roes. & Schult) (Palouse Prairie)

Present in various seral stages of montane coniferous forest and extending also into the chaparral:

Castilleja angustifolia (Nutt.)
Odostemon repens (Lindl.)
Sophia fillipes (A. Gray)
Gilia aggregata (Pursh)
Delphinium menziesii DC.
Mertensia brevistyla S. Wats.
Agoseris taraxacifolia (Nutt.)
Wyethia amplexicaulis (Nutt.)
Nemophila breviflora A. Gray
Balsamorhiza sagittata (Pursh)
Hedysarum utahensis Rydb.
Lithophragma parviflora (Hook.)
Senecio crassulus A. Gray
Senecio cymbalariodes Nutt.
Drymocallis glandulosa (Lindl.)
Geum strictum Ait.
Valeriana occidentalis Heller
Lappula floribunda (Lehm.)
Symphoricarpus vaccinioides Rydb.
Amelanchier alnifolia Nutt.
Prunus melanocarpa (A. Nels.)
Acer grandidentatum Nutt.
Populus tremuloides Michx.
Ceanothus velutinus Dougl.
Geranium fremontii Torr.
Phacelia heterophylla Pursh
Erigonum heracleoides Nutt.
Stipa lettermani Vasey
Stipa columbiana Maxoun
Poa curta Rydb.
Agropyron subsecundum (Link)
Festuca kingii (S. Wats.)
Carex geyeri Buott. (Elk Sedge)

PRAIRIES AND PASTURES OF THE DISSECTED LOESS PLAINS OF CENTRAL NEBRASKA*

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* Contribution No. 152 from the Department of Botany, University of Nebraska. This study was aided by a grant from the University Research Council, University of Nebraska.

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PRAIRIES AND PASTURES OF THE DISSECTED LOESS PLAINS OF CENTRAL NEBRASKA*

INTRODUCTION

Lying north of the great southward bend of the Platte River in central Nebraska but southeast of the sandhills, there are several thousand square miles of rugged uplands known as loess bluffs. They are quite unlike the sandhills with their typical cover, largely of postclimax tall grasses. They also differ widely from the Nebraska plain eastward and southeastward where mid-grass or true prairie clothes the level or slightly undulating land. The vegetation of the sandhills has been studied only recently, by modern methods, in its relation to soils and climate (Tolstead 1942). The mixed prairie southward has undergone extended examination throughout a complete drought cycle (Albertson 1937; Albertson & Weaver 1942; Weaver & Albertson 1943, 1944). But the excellent cover of grasses and forbs of the mixed prairie, which clothes and protects the highly erosive loess bluffs and furnishes sustenance for thousands of cattle, has thus far not attracted the attention of an ecologist.

This preliminary survey is concerned with soil and aerial environment of the abundant undisturbed native vegetation, and its composition and behavior in the extensive range lands. It also includes a 3-year study of grazing types, of grazing patterns throughout the season, and of forage yield and forage consumption in experimental pastures.

GEOLOGY

The area between Broken Bow, Ord, Grand Island, Kearney, and Lexington encompasses parts of two principal physiographic regions, the Central Nebraska Dissected Loess Plains and the Platte River Lowland-Terraceland regions. However, most of the area lies within the Dissected Loess Plains region which is separated into subregions by relatively narrow strips of terracelands and lowlands along the South Loup and Middle Loup River valleys and minor drainages which are largely tributary to the Loup Rivers and in part tributary to the Platte River.

The Central Nebraska Dissected Loess Plains grade transitionally into the Sandhills region to the north and northwest. They are bounded by the Platte River Lowland and Terraceland region on the south and merge with the Loess and Drift Hill regions eastward and northeastward beyond the limits of the area under discussion.

The area is developed principally on mantlerock materials of Pleistocene age with occasional small areas, principally along valley sides, where the limy sandstones of the Ogallala formation of Pliocene age are exposed.

A period of general uplift and extensive erosion followed the deposition of the Ogallala sediments, and the Ogallala formation was carved into hills and valleys of considerable relief, approaching 150 feet or more in places. The post-Pliocene drainage pattern appears to be distinct from the present drainage pattern.

In early Pleistocene time the lower parts of the post-Pliocene valleys were filled with alluvial sands and gravels capped with silts. These sediments were deposited during the time when the first continental glaciation (the Nebraskan) invaded the eastern part of Nebraska and when the earliest mountain glaciation was an important factor in the mountainous areas to the west and northwest of Nebraska. This glacial epoch was followed by a period of weathering and soil development which in turn was followed by a second major glaciation (the Kansan).

During early Kansan time a second cycle of erosion and sedimentation began. It was similar to the preceding (Nebraskan) cycle but was probably along a somewhat different and changing drainage pattern. This channeling and filling removed some of the materials deposited in Nebraskan time and filled the Kansan valleys up to levels generally above those of the Nebraskan sedimentation. The Kansan glacial epoch was followed by a second period of weathering and soil development. Thus, a constructional topography was built which tended toward decreasing the general relief of the area and toward the establishment of a high sloping plain surface, which is reflected today in the high plain remnants which are scattered throughout this topographic region.

The trend during middle and later Pleistocene time in this region has been toward greater down-cutting and lesser valley filling, which is more closely related to the present drainage pattern, with the development of narrower and successively lower valleys. Moreover, the interfluve areas received relatively thick mantles of wind-blown dust known as loess, much of it being blown up from the alluvial flats along the through valleys of the region. There were two principal periods and one or more minor ones of loess accumulation separated by periods of weathering and soil development. Near important source areas, the loess accumulated rapidly and formed relatively thick deposits. Farther from important source areas, the loess accumulated more slowly, it formed thinner deposits and underwent more weathering during accumulation.[1]

It has been concluded by Condra, Reed, and Gor-

[1] The writers are indebted to Mr. E. C. Reed, Associate Director of the Nebraska Conservation and Survey Division, for this geological description.

don (1947) that comparatively little loess was formed in Nebraska when sediments were being released from mountain glaciers and fresh till sheets. Lugn (1935) has shown that the Sandhill region has released much Tertiary and Pleistocene loess-forming material which was blown prevailingly eastward and southeastward contributing directly or indirectly to Loveland and Peorian deposits in a broad area east of the sandhills. Condra, Reed, and Gordon (1947) state that Nebraska loess was developed from various dry-land areas having fine sediments and that little of it came directly from fresh till and glacial outwash. They find that most loess deposition in Nebraska correlates with interglacial time and that wind, correlated with other factors, is the major force in the genesis of loess.

The aggregate thickness of the loess mantle in this area, especially near the principal valleys, is relatively great, approaching 150 feet or more in places. Headward erosion into these areas of thick loess mantle rapidly develops the characteristic canyon topography of the region. As soon as the sod and soil cap of the upland plain is removed by undercutting, the relatively coarse silts of the underlying loess are subject to rapid erosion by water because of their silt texture and lack of cementation, and near-vertical canyon walls result. Such walls along water courses, roads, and in other places subject to erosion are common (Figs. 1 and 2). Moreover, weathering of the canyon wall tends to induce a vertical or near-vertical cleavage in the loessal materials forming lines of weakness along which the loess tends to slide downward. This results in the "catsteps" which are so typical of the side slopes of the uplands in this region (Figs. 3 and 4).

Catsteps are not only a prominent feature of the landscape, but they also greatly affect the distribution of the various types of vegetation. Hence, a knowledge of their origin is of considerable importance. According to Mr. E. C. Reed, catsteps are caused by the textural variations and the groundwater relationships within the loess and most commonly occur near the contacts between older and younger loesses, as at or near the Loveland-Peorian contact. The Loveland loess accumulated rapidly as a thick mantle over this region and its deposition was followed by a relatively long period of weathering and soil development. Thus a dark surface soil with a clayey subsoil was developed at the top of the Loveland. This differs greatly in texture and permeability not only from the coarse silt of the middle and lower parts of this loess but also from the lower and middle parts of the Peorian loess which was deposited upon it during a later period of loess accumulation. Under these conditions water from precipitation tends to move downward, often 30 to 40 feet, through the Peorian loess with comparative ease until the Peorian-Loveland contact is reached where permeability is greatly restricted and the groundwater movement is directed laterally toward

FIG. 1. View in the northwestern portion of the dissected loess plains showing the bluffs and rolling land characteristic of the area. The loess soil is protected by a thick carpet of blue grama *(Bouteloua gracilis)*, a cover of western wheat grass *(Agropyron smithii)*, or by other vegetation.

FIG. 2. A small flat-bottomed valley showing three nearly vertical canyon walls in the background as a result of natural erosion and slipping of the loess. Western wheat grass is on the canyon floor and scattered white elms *(Ulmus americana)* are on the slopes. Photo near Broken Bow, Nebr.

the valley or canyon sides where it is discharged as springs and causes the overlying Peorian loess to slip and slide valleyward. Catsteps are thus developed successively near the Loveland-Peorian contact and blocks of Peorian loess are moved down the valley sides below the Loveland-Peorian contact level.

PHYSIOGRAPHY

The general physiography is that of an upland plain, ranging from almost level to steeply rolling or hilly land. The average elevation of the plain is about 2,200 feet above sea level. It is traversed by numerous low-lying strips of flat alluvial land along the rivers and larger streams. Stream erosion and wind action have produced considerable relief. Over the greater part of the area the upland plain has been thoroughly dissected. It is now hilly. The hills are often 100 to 150 feet higher than the valleys between them (Fig. 5). The comparatively level areas are not extensive. They occupy the highest positions and occur principally near the center of the divides where the original constructional plain has escaped destructive erosion. Such areas are locally known as tablelands. The tableland areas are very gently undulating or almost flat and are modified in places by small sinks or depressions. Nearly all of the area is well drained by rivers and streams flowing southeastward into the Platte River. Chief among these are North, Middle, and South Loup Rivers, and Wood River. Not only is the greater part of the region thoroughly drained but over large areas runoff is excessive and erosion is severe.

CLIMATE

This portion of the mixed prairie has a climate characterized by moderately long, cold winters and a fairly long growing season with hot summers. The growing season usually includes 140 to 155 days without severe frost and extends from early May until early October. During the summer the average day temperatures sometimes reach 90° F. At such times the maximum daily temperature reaches or even exceeds 100°. Minimum temperatures of 15° to 20° or more below zero occur at intervals during the cold season when the vegetation is dormant. Mean annual temperature is about 48° F.

The mean annual precipitation is 23.1 inches at Broken Bow in the northwest and 23.9 at Kearney on the southern edge of the loess hills. Its distribution is of the Great Plains type, nearly 80 percent occurring between April 1 and September 30. The greater part of the summer rainfall occurs during local thunderstorms. Often the rainfall is very heavy over a short period of time. In May and June periods of drought are uncommon, in July the distribution of rainfall is less favorable, and during August and September long periods of drought sometimes cause reduced yields even of the crop of native grasses.

FIG. 3. (Upper) Typical catsteps on the side of a valley. These steps are 3 to 10 feet wide. Catsteps vary from 1 to 15 or more feet in width. On such areas both mid grasses, as side-oats grama *(Bouteloua curtipendula)* and little bluestem *(Andropogon scoparius)*, and tall grasses, especially big bluestem *(A. furcatus)*, are common. Photo near Kearney. (Lower) View of catsteps in the McCan experimental pasture near Kearney, Nebr.

FIG. 4. Closely grazed range of blue grama north of Broken Bow showing hillside with much slumping of the soil to form catsteps.

Snowfall is light, about 26 inches. Much of the snow is swept by winds into depressions, unless it lodges in a cover of grass, and thus often contributes but little to the supply of moisture of the soil upon which it falls. Wind movement is fairly constant and often high. It is an important factor in promoting water loss. Humidity is relatively low and

FIG. 5. Hilly range land between Broken Bow and Round Valley with the herd of cattle about the artificial pond in the ravine. This land is very easily eroded.

evaporation is high during summer and fall. The mixed prairie is typically a land of sunshine; the proportion of clear days is high. The climate is well suited to the production of hay and grain crops and to the raising of livestock.

SOIL

Deposits of loess once covered the entire area in a smooth, thick mantle. These were later eroded and in places entirely removed by stream action. In its unweathered condition, the loess is uniform in texture and is composed largely of particles of silt. It varies in color from brownish yellow to yellow or almost white. Lime is abundant and a small quantity of iron stains the material in many places.

This area is in the part of the mixed prairie where the precipitation is moderate. The soils of the region have been leached of their carbonates and other easily soluble compounds to depths ranging up to about 3 feet. The most striking characteristic of most of the soils is the dark color of their surface layers. This results from the presence of organic matter or finely divided carbonaceous material, derived largely from the decayed roots of vegetation and intimately mixed with the mineral part of the soil. The color varies with the quantity of organic matter present. Soils are usually darkest on the flatter areas and in the depressions where an abundance of moisture has especially favored the growth and decay of vegetation and where the position has prevented the removal of the organic matter through erosion. (*cf.* Hayes, *et al.* 1928).

Throughout the well drained, gently undulating or rolling areas where soils are kept in a relatively "young" state through gradual accretion of fresh materials (chiefly through wind action), conditions have favored the accumulation of organic matter. In this region soils are constantly rejuvenated by deposition of wind-blown dust and by the activities of burrowing animals (Thorp 1948). The soils have adjusted themselves to the climatic and vegetal environment and will retain approximately their pres-

ent characteristics as long as the present natural conditions prevail.

HOLDREGE SILT LOAM

The well developed soils of uplands are predominately those of the Holdrege series. They have developed from loess. The profile shows three main layers or horizons—the surface soil or A horizon, the B horizon or subsoil, and the parent material or the C horizon. The various horizons vary somewhat in thickness from place to place. A representative monolith sample from the southern part of the area is described.

A large trench was dug in a pasture where experiments were conducted in the loess bluffs area one mile north of Kearney (Fig. 6). This was in typical Holdrege silt loam. Both soil and rooting habits of plants were studied to a depth of 6 feet. The land was very gently sloping and the soil was mature. The first inch of dark grayish brown silt loam consisted of dust which had blown in from adjacent fields but was held firmly in place by the dense cover of buffalo grass. The A_1 horizon of friable dark grayish brown silt loam extended to a depth of 12 inches. It varied from fine crumb to medium granular structure and showed vertical cleavage. This is the horizon in which organic matter accumulates at or near the surface. The organic matter which gives this layer its dark color is thoroughly mixed with the mineral constituents and there is practically no color change (in the upper 6 inches) when the soil material is crushed (Table 1).

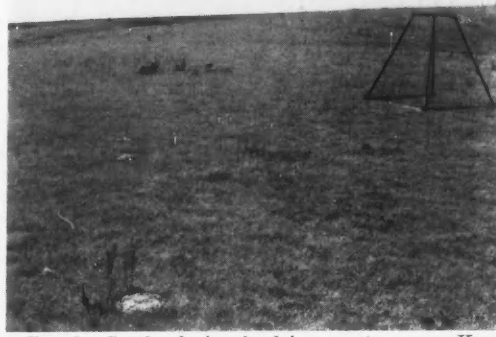

FIG. 6. Gently sloping land in a pasture near Kearney. The Holdrege silt loam is covered with a thick mat of buffalo grass *(Buchloe dactyloides)*. The movable exclosure (30 square feet in area) is one of many used in ascertaining yield and consumption of forage.

TABLE 1. Monolith sample of Holdrege silt loam from Kearney, Nebraska.

Horizon	Inches from surface	COLOR[1] Dry	COLOR[1] Moist	Texture	Structure	Consistence (moist)	pH by Soiltex
Recent dust accumulation	0-1	Grayish brown 10YR 5/2	Dark grayish brown 10YR 3/2	Silt loam	Fine crumb (soft fine grains)	Friable	6.5
A_{1-1}	1-6	Grayish brown 10YR 4/1.5	Dark grayish brown 10YR 3/1.5	Silt loam	Fine crumb; vertical cleavage	Friable	6.5
A_{1-2}	6-12	Grayish brown 10YR 4/2	Dark grayish brown 10YR 3/2	Silt loam	Strong, fine to medium granular; vertical cleavage	Friable	6.8
B_1	12-15	Grayish brown 10YR 4/2	Dark grayish brown 10YR 3/2	Light[2] silty clay loam	Prismatic-nuciform-granular (compound) with strong vertical cleavage	Slightly plastic	6.8
B_{2-1}	15-22	Grayish brown 10YR 5/2	Grayish brown 10YR 4/2	Silty clay loam	Do. primary aggregates ½ to ¾ inch in diameter	Moderately plastic	7.0
B_{2-2}	22-28	Light brownish gray 10YR 6/1.5	Grayish brown 10YR 5/1.5	Silty clay loam	Imperfect prismatic-nuciform	Moderately plastic	7.0
B_3	28-36	Light yellowish brown 2.5Y 6/3	Yellowish brown 2.5Y 5/3	Heavy[2] silt loam	Imperfect prismatic; weakly nuciform secondary aggregates	Slightly plastic	7.5
Bca[3] or C_1	36-48	Mottled pale yellow and white 2.5Y 7/4, 8/1	Light yellowish brown 2.5Y 6/3	Silt loam	Prismatic to massive	Friable	8.0; soft lime carbonate; lime concretions

[1] Provisional Soil Survey color names, based on standard Munsell color charts; e.g. 10YR 5/2 means: hue 10 yellow-red; value on lightness scale is 5; chroma saturation is 2. The color names are those in common usage.
[2] "Light" silty clay loam means that the soil has near the minimum of clay content for that texture class; "heavy" silt loam has a maximum of clay allowable for silt loam.
[3] The main C horizon or "parent material" was not reached in this sample.

The B_1 horizon, which is transitional from the lighter textured surface soil to the heavier textured subsoil, occurred between 12 and 15 inches in depth. This light silty clay loam was slightly plastic and showed strong vertical cleavage. The B_2 horizon of grayish brown silty clay loam showed moderate plasticity. It occurred at a depth of 15 to 28 inches. This is the horizon of maximum clay development or accumulation. Here the coating of organic matter around the soil granules becomes thinner. When the soil is cut with a sharp instrument or the materials are crushed, the lighter interior of the granules is exposed and the soil becomes lighter in color.

The B_3 horizon (28 to 36 inches depth) occurred just above the horizon of lime accumulation. It is a yellowish brown, heavy silt loam. The layer of lime accumulation, characteristic of Chernozems, began at 36 inches depth and extended to about 6 feet. This was the approximate depth of the solum, below which the C horizon of parent material was encountered. This was yellowish-brown, friable, silty, structureless material which contained much lime. The pH increased gradually from 6.5 in the first foot to 7.0 in the second, but was 7.5 to 8 at greater depths.

We are indebted to Mr. James Thorp, Principal Soil Correlator, Great Plains States, U. S. Division of Soil Survey, for a complete description of monoliths of soils (Tables 1 and 2) which were brought to the laboratory for study.

Colby Silt Loam

Over much of the area, the Colby soils occupy the greater portions of the uplands. "The light-colored Colby soils may be regarded as immature. Constant erosion has prevented the accumulation of much organic matter and as the surface water flows rapidly from the slopes, leaching of the carbonates from the subsoil does not proceed faster than the new material is exposed as a result of erosion. The surface layer is thin and lighter in color than that of the Holdrege . . . soils.

"Colby silt loam is grayish brown, light grayish brown, or ash-gray friable silt loam from 4 to 8 inches deep. The upper part of the subsoil is of similar or slightly lighter color, but is identical in texture and structure. . . . On the more gradual slopes and more rounded divides, conditions have favored growth and decay of vegetation. Here the surface soil is deeper and darker than typical. On steeply sloping areas, erosion has prevented the accumulation of organic matter and the soil is consequently light in color. In many places the surface layers have been entirely removed by erosion, exposing the light, yellowish-gray parent loess [Fig. 7]. . . . Areas of this land vary from rolling to extremely rough and dissected. Even areas of moderate relief are dissected by numerous intermittent streams which have cut deep and, in places, almost perpendicular-walled valleys. Soil slipping is common in rougher areas, and the slopes in many places present short vertical exposures having a step-like

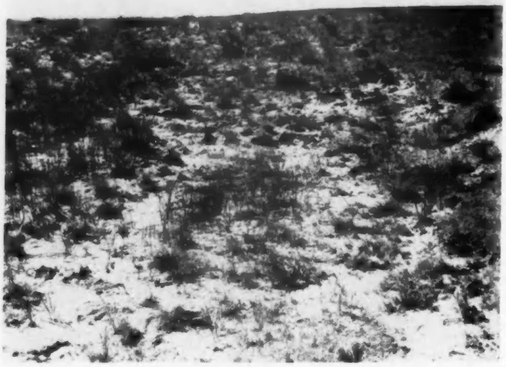

Fig. 7. Colby soil exposed on an eroding slope. The chief grasses are purple three-awn (*Aristida purpurea*) and western wheat grass.

appearance. Drainage is everywhere thorough and in most places excessive." (Hayes *et al.* 1928.)

Colby soils have neither a horizon of compaction nor one of lime accumulation, but the grayish-brown surface soil rests directly upon the light-colored parent loess.

The surface soil of Colby silt loam extends to an average depth of 6 inches. In the following profile the depth is 4 inches, exclusive of the A_{1-3} transitional horizon in which the soil properties are more like those of the A than the B horizon (Table 2).

The soil profile of Colby silt loam was examined on a moderately sloping hillside in a large pasture 5 miles southeast of Broken Bow (Fig. 8). It supported a good cover of blue grama (*Bouteloua gracilis*).[2] The surface 0.75 inch is a friable, dark grayish brown soil with a medium to fine crumb structure. This A_{1-1} horizon, which seldom exceeds a few inches in thickness, has accumulated more organic matter and is consequently darker in color than any other horizon. The second horizon (A_{1-2}) is usually about 4 inches thick. In texture it is similar to the soil above but the color is lighter and the soil is weakly granular. The A_{1-3} transitional horizon is a dark grayish-brown, heavy silt loam of granular structure with prismatic cleavage.

The subsoil (B_1 horizon) composes much of the second foot in depth. It is a light silty clay loam, grayish brown in color with considerable plasticity and a nut-like granular structure. Characteristics of the parent material are given in Table 2. The pH value to a depth of 20 inches was 7.0 but increased to 7.5 or 8.0+ in the parent material which was rich in lime.

Analyses of Soils

Mechanical analyses were made of the Holdrege silt loam soil in the McCan pasture near Kearney

[2] Nomenclature of grasses follows Hitchcock's "Manual of the Grasses of the U. S.," that of other species is according to Britton and Brown's "Illustrated Flora," unless other authority is given.

TABLE 2. Monolith sample of Colby silt loam[1] from Broken Bow, Nebraska.

Horizon	Inches from surface	Color[2]		Texture	Structure	Consistence	pH by Soiltex
		Dry	Moist				
A_{1-1}	0-3/4	Grayish brown 10YR 4/2	Dark grayish brown 10YR 3/2	Silt loam	Medium to fine crumb	Friable	7.0
A_{1-2}	3/4-4	Grayish brown 10YR 5/2	Grayish brown 10YR 4/2	Silt loam	Granular or crumb	Friable	7.0
A_{1-3}	4-12	Grayish brown 10YR 4.5/2	Dark grayish brown 10YR 3.5/2	Heavy silt loam	Granular with prismatic cleavage	Friable, moist; slightly plastic wet	7.0
B_1	12-20	Grayish brown 10YR 5/2	Grayish brown 10YR 4/2	Light silty clay loam	Medium prismatic-nuciform-granular[3]	Slightly plastic, moist, to plastic, wet	7.0
C_1	20-32	Olive brown 2.5Y 5.5/3	Dark olive brown 2.5Y 4.5/3	Silt loam	Prismatic-coarse nuciform	Friable	7.5
C_2	32-46	Light olive brown, mottled yellowish brown 2.5Y 6/3, 10YR 5/4	Grayish brown, mottled yellowish brown 2.5Y 4.5/2, 10YR 4/4	Silt loam	Coarse prismatic	Friable	8.0 (Calcareous)
C_3	46-48+	Light brownish gray, mottled white 2.5Y 6/2, 9/2	Grayish brown, mottled white 2.5Y 4.5/2, 8/2	Silt loam	Coarse prismatic grading to massive	Very friable	8.0+ (Calcareous)

[1] This soil has been called Colby silt loam over a wide area in Nebraska, but it is darker colored than the Colby silt loam of eastern Colorado and western Kansas. It also contains more clay in the B horizon than is typical of Colby silt loam. It resembles closely the Ulysses silt loam, a series recognized tentatively in western Kansas.
[2] Provisional Soil Survey color names, based on Munsell color charts.
[3] Most soil structure is complex, including large aggregates that fall apart into smaller ones of different shapes.

FIG. 8. Typical range land near Broken Bow. The soil is Colby silt loam and the chief grass is blue grama. Note the catsteps which cause a rough surface (darker) on the hillsides.

and of a small area of Holdredge silt loam from a second pasture 5 miles west of Kearney (Sheen pasture), where studies on yield and consumption of forage were made. The hydrometer method as described by Bouyoucos (1936) was used, but with slight modifications (Table 3).

The two soils are somewhat similar. Both are very fine textured. The second is less deeply developed, but it has the more pronounced accumulation of clay.

TABLE 3. Mechanical analyses of soils. The percentage of the clay fraction less than 0.002 mm. is also included in the material less than 0.005.

Depth, inches	Percentage of oven-dry soil			
	Sand > 0.05 mm.	Silt .05 to .005 mm.	Clay <0.005 mm.	Clay <0.002 mm.
(1) From McCan Pasture				
0-6	14.4	59.4	26.2	23.6
6-12	16.4	53.2	30.4	25.8
12-24	15.4	52.4	32.2	33.7
24-36	9.0	52.7	38.3	35.8
36-42	15.0	52.1	32.9	29.4
(2) From Sheen Pasture				
0-6	19.3	54.0	26.7	24.1
6-12	15.7	51.7	32.6	30.4
12-24	11.9	48.2	39.9	37.8
24-36	8.7	51.3	40.0	37.8
36-42	15.9	58.9	25.2	22.1

The percentage of aggregation of these soils as determined by the hydrometric method, and the percentage of organic matter and nitrogen as determined by the modified Walkley-Black method are shown in Table 4.

An examination of the data in Table 4 reveals that the first soil has only moderate aggregation and

Table 4. Percentage of aggregates greater than 0.25 mm. (based on oven-dry weight), organic matter, and total nitrogen in soils in Table 3. U, upland; S, moderate slope.

Depth	(1) McCan pasture	(2) Sheen pasture	Depth	McCan pasture		Sheen pasture	
				Organic Matter	Total N.	Organic Matter	Total N.
	percent	*percent*					
0-2	21.3	14.0	0-4 U	5.17	.170	4.38	.159
2-6	22.1	13.9	4-12	4.13	.137	4.07	.141
6-12	20.2	18.0					
12-24	24.5	17.3	0-4 S	4.46	.161	5.11	.194
24-36	17.7	13.1	4-12	4.09	.143	3.29	.110
36-40	14.2	11.1					

is not very stable. Aggregation in the second soil is low and this soil is even less stable. For example, at Lincoln, Nebraska, on the Experimental Farm the topsoil (upper 6 inches) under native grasses has a degree of aggregation of 80 percent (Bertramson and Rhoades 1938). In the first soil, the 24.5 percent aggregation corresponds to the silty clay loam texture shown in Table 1. In the second, the greater aggregation at 6 to 24 inches corresponds to the presence of the layer of heavy silt loam and light silty clay loam at this depth. Although at these depths the clay and organic matter produce maximum aggregation, at 24-36 inches the increased clay content is not accompanied by increased aggregation. The decrease in influence of organic matter is likewise seen in comparing the 0-6 inch depth with the 6-12 inch. A large decrease in organic matter is not accompanied by much change in aggregation.

Both soils are low in organic matter and in total nitrogen. Since the coefficient of correlation between the Walkley-Black method and the modified Robinson method is very high (Smith and Weldon 1940), the results may be compared with others determined by the latter method. Shively and Weaver (1939) report a percentage of organic matter of 4.18 to 4.56 in native prairie at Holdrege, Oxford, and at another station in the Holdrege soil series under an average precipitation of about 23 inches. The percentage of nitrogen ranged from 0.178 to 0.206. Similar data from Lincoln and other stations in eastern Nebraska in the same soil series (precipitation about 29 inches) gave a percentage of organic matter of 6.07 to 6.25, and 0.260 to 0.278 percent of nitrogen. All the preceding samples were from a depth of 0-4 inches.

Erosion

The erosiveness of these fine textured soils is very high and the need of a continuous protective cover of grass is correspondingly great. There is some constant erosion by wind and water from these steep bluffs, but when the cover is broken by grazing or trampling, erosion almost immediately becomes serious. Except in years of drought, the ranges—at least the larger ones—are permitted to retain a reasonable amount of uneaten forage and a thin layer of debris on the soil. But this does not maintain under close grazing, and in the best ranges trampling results in the formation of paths which often develop into deep gullies. These are usually the long trails from the distant portions of the range. They are used regularly by the livestock traveling to and from the wells or ponds where they obtain water (Fig. 9). However, paths are made in grazing steep banks and in passing from one valley to another.

Fig. 9. A few of the many paths leading to the windmill. Note on the left the beginning of new paths on both sides of the older one which is several inches deep.

At first the soil is compacted in the paths, then the grass dies. Next the foot-wide paths begin to erode. The soil, loosened by trampling, blows away or is washed away and the paths are deepened by rains. As the depth increases to several inches the path is abandoned and a new, more or less parallel one is made. But erosion continues and a ditch three

Fig. 10. Deeply eroded parallel paths in loess. Dark places in path on left are 40 inches deep. The general cover is buffalo grass but hairy chess *(Bromus commutatus)* grows thickly in portions of the old path. The second path is 11 inches deep and is being abandoned for a new one on the right, in which some grass still grows.

or more feet deep may be formed (Fig. 10). The banks cave, the debris is washed away, and from the old path or series of paths deep eroded areas a rod to several rods in width may result.

The cutting back of a ravine to near the top of the bluff and its joining a similar ravine on the opposite side and thus dissecting the hill or range of hills is not uncommon (Figs. 11 and 12). It is frequently aided by the trampling of livestock. In one of the experimental pastures where the well was near the far end of the second 80 acres of the quarter section, the cattle continuously trailed up one ravine, over a steep ridge, and down another. These paths were, in a few years, eroded so deeply that it became difficult to drive from the gate in the near end of the pasture to the more distant part. Only a few rods separated two other favorite grazing grounds on lowlands on two sides of a long steep ridge. Although deep paths had not yet been formed, there was much trampling and thinning of the cover where the herd was observed several times passing over the ridge between these two grazing grounds.

FIG. 11. Undercutting of Holdredge silt loam in the McCan pasture near Kearney. The valley floor is clothed with a dense cover of buffalo grass, but floodwaters pour over the bank and undermine the soil which is then pulled down by gravity. Note the catstep on the right and the loose soil which has fallen from the bank.

ROOT RELATIONS

Previous studies had led the writers to believe that in these mellow soils of normally moderately low water content, roots of the native plants would penetrate deeply (Weaver 1919). Several years of good precipitation following the great drought of 1933 to 1940 has resulted in complete replenishment of subsoil moisture. The examination of root systems in several sites confirmed this belief.

Buffalo grass (*Buchloe dactyloides*) was studied near Kearney in Holdrege silt loam. The roots were traced in the walls of a trench excavated on nearly level land, some to a depth of 6 feet where they ended after extending well into the lime layer. The soil was moist to only about 5 feet. In one end

FIG. 12. Typical gulley which has eroded far toward the top of the hill. Light colored soil is exposed at various places along the steep banks. This is typical loess-bluff topography.

of the trench where the water had penetrated to only 4.5 feet, no roots were found beyond this depth.

A monolith of the soil 12 inches wide, 4 feet long, and 3 inches into the vertical wall of the trench was obtained without injury to the soil structure or grass roots. By means of long soaking and careful washing, the soil was finally removed from the roots. They were then arranged under water in their natural position, transferred to a black background, and photographed (Fig. 13). The great bulk of the roots grew so nearly vertically downward that practically all that extended into the second foot reached the bottom of the 3-inch-thick monolith. Although these fine, tough roots were branched throughout their length, the greatest number and the best branching occurred in the A soil horizon and its transition to the B horizon, that is, to a depth of 15 inches. The leafy shoots were lightly grazed to a height of 2.5 inches.

Studies of root depth and distribution were made in Colby silt loam half way down a steep hillside (slope 15 percent). At a depth of 19 inches a darker layer proved to be the top of a buried soil. The wind-carried Peorian loess had been deposited over a mature soil formed from the upper portion of previously deposited Loveland loess. This dark layer was 10 inches deep. The second layer of old "topsoil" seemed to stimulate greater root branching. The mass of buffalo grass roots was very dense to 52 inches. Roots in this very moist soil were numerous to 5 feet, and some reached 6 feet 3 inches in depth.

Further excavations were made in Colby silt loam in other prairies about 5 and 7 miles, respectively, northwest of Kearney. The roots of a dense stand of western wheat grass (*Agropyron smithii*) were examined on a hillside. They nearly all penetrated vertically downward, some extending into the moist subsoil to 10 feet and 3 inches, where the clear, white root tips were found. They were identical with those

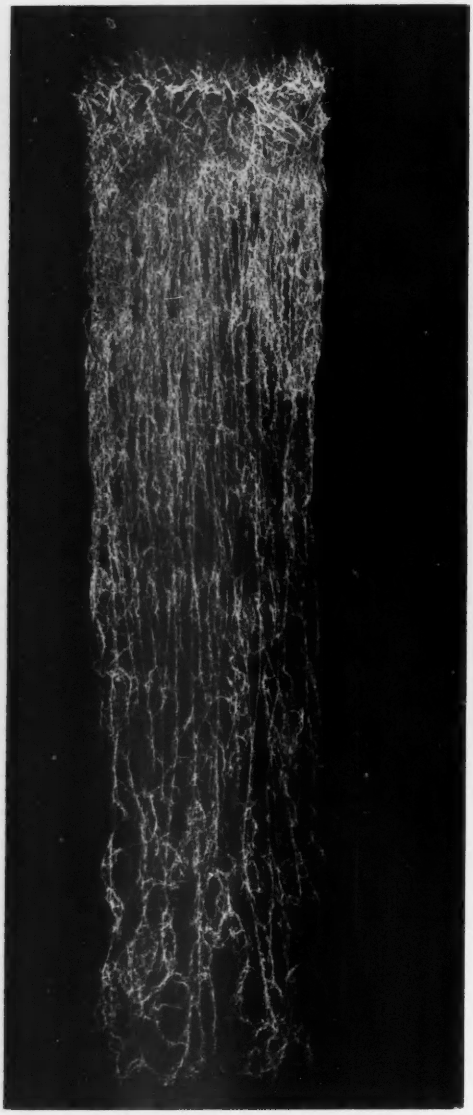

FIG. 13. Roots of buffalo grass to a depth of 4 feet. Note their greater number and more profuse branching in the surface 15 inches of soil. Note also the branching habit in the deeper soil.

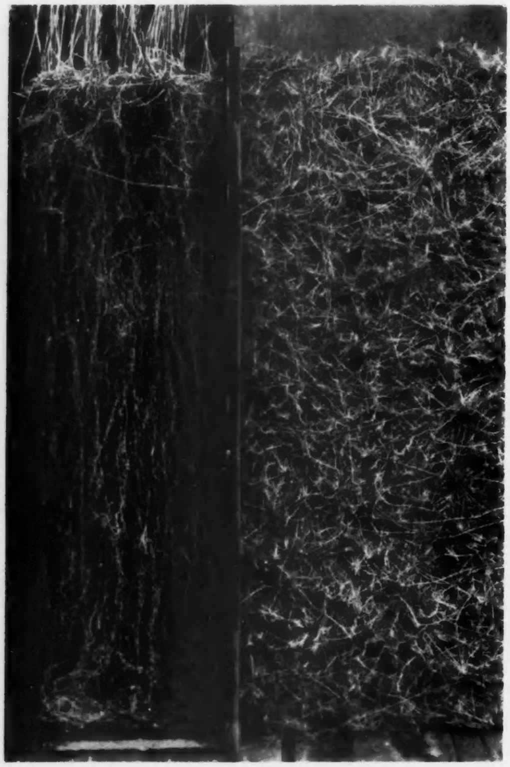

FIG. 14. (Left) Upper portion of the root system of western wheat grass growing in Carrington silt loam, washed from a soil monolith 12 inches wide, 40 inches deep, and 5 inches thick. (Right) Roots and rhizomes of this grass in the surface 10 centimeters of a half-square meter of soil. Excavations made by George A. Garrison.

excavated in Wabash silt loam at Lincoln (Fig. 14). Roots of big bluestem in this Colby soil were abundant at 7.5 feet depth and a few were traced to 8 feet. But these root depths were exceeded, as usual, by those of certain perennial forbs.

The tap root of an old plant of few-flowered psoralea *(Psoralea tenuiflora)* was 1.5 inches in diameter near the soil surface and, after some branching, ⅝ inch thick at 9 feet in depth. At greater depths it gave off several branches, some of which were traced 6 feet deeper but not to their ends. Tap roots of several mature plants of *Lygodesmia juncea* attained depths greater than 16 feet.

Roots of blue grama were examined in prairie in the same soil type about 2 miles distant. These roots were very similar to those of buffalo grass in fineness, branching, and depth of penetration. They were abundant in the limy, moist, loess subsoil to about 6 feet and the longest penetrated a foot deeper.

Roots of blue grama were also examined in Colby silt loam about 5 miles southeast of Broken Bow. They were from undisturbed native prairie. Depth of penetration was approximately 5.5 feet. They ended in a very moist, limy subsoil. Those obtained from a 3- by 12-inch monolith 4 feet deep are shown in Figure 15. It may readily be seen that the greatest concentration of roots was in the A horizon (0-12 inches), but they were also abundant in the next 8 inches or B horizon. They were least abundant below 3 feet. From these studies and numerous other observations it seems clear that the important grasses are well rooted to depths of 4 to 6 or more feet, and that many of the forbs extend to much greater depths.

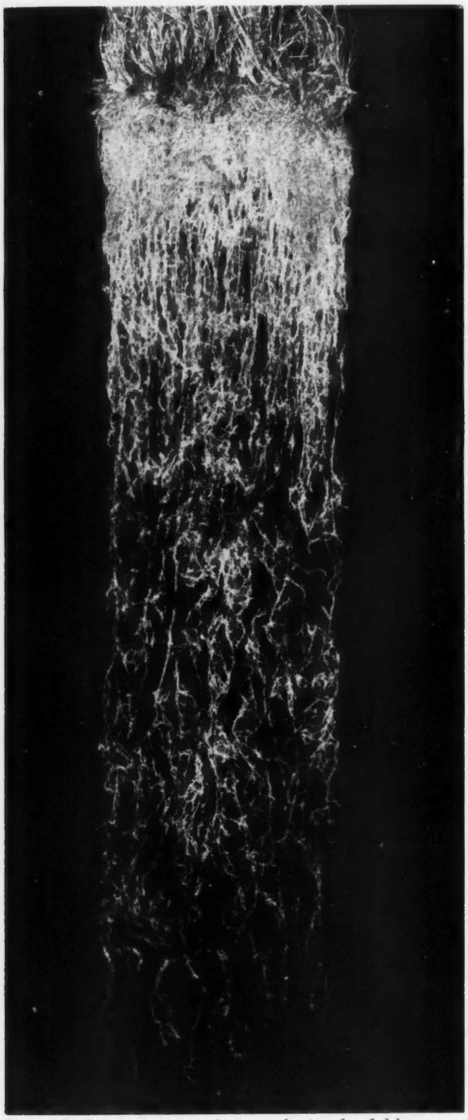

FIG. 15. Root system of a good stand of blue grama growing in Colby silt loam near Broken Bow, Nebr. Note the concentration of roots in the A horizon.

EARLY SETTLEMENT AND LAND USE

Although the first settlement in this grassland area was made in Buffalo County in 1858 and the Union Pacific railroad was built in the Platte Valley just south of the loess bluffs in 1868, general settlement of the area (except by cattlemen) began considerably later. Prior to the coming of the cattlemen to Custer County in 1869-70, for example, most of the county was occupied by Indians who subsisted largely on wild game, fish, and fruit. But during the 4 or 5 years after 1870, cattle grazed on the free open range, where a variety of nutritious grasses afforded good forage in summer and fair winter grazing. By 1872-74 the early settlers in the several counties located in the larger stream valleys where there was an abundance of fuel and water, but later settlement spread throughout the uplands. By 1890 most of the land was homesteaded and the fencing of range land became general. The rougher parts of the eroded loess plain are now held in large tracts by livestock farmers and ranchers, many of whom cultivate only a small portion of the land. But even very rolling land is used for growing corn, small grains, alfalfa and other crops (*cf.* Hayes *et al.* 1926).

Since the homesteads were relatively small (160 acres in area) and inadequate for a large herd of livestock, there seemed no choice in making a livelihood but to break the least rolling land and to grow farm crops. In many places this resulted in greatly accelerated erosion, the loss of the topsoil, and an extremely rough soil surface. More recently such fields were sown to sweet clover with the hope of increasing the nitrogen supply and aiding nature in her struggle to reclaim the soil. These lands are reclaimed very slowly, especially where grazing is practiced. A long subsere of annual weeds, short-lived unpalatable grasses, and perennial weeds may, after 15-30 years, be replaced by open stands of buffalo grass, sand dropseed (*Sporobolus cryptandrus*), western wheat grass, and other perennials. But the incomplete stands and meager yields reveal clearly that organic matter is still low and nitrogen supply is scarce.

The extent of the land in each county still under a cover of grass (nearly all native grasses) and the percentage that should be placed under grass, according to the Federal-State Soil Conservation and Survey Division, are shown in Table 5.

Since portions of two of these four counties in the loess bluff region are adjacent to or covered in part by the sandhills, it is necessary in Table 5 to deal only with non-sandy soils. The total area of these counties varies from about 566 square miles (Sherman and Valley) to 2,588 square miles (Custer). Hence the areas in grass are very large. The first column in Table 5 shows that about a fourth to nearly a half of these counties are still natural grassland. The large percentages recommended for a grass

TABLE 5. Percentage of uncultivated land, total non-sandy uplands in grass, and total non-sandy uplands recommended to be placed under grass. Percentages are based on the area of the county.

County	Uncultivated land (exclusive of riverwash and sand hills). Nearly all grassland	Total non-sandy uplands in grass. Dominant slope more than 10 percent	Total non-sandy uplands recommended for grass
Buffalo	25.9	14.3	32.5
Custer	44.9	38.2	47.4
Valley	48.3	41.5	51.4
Sherman	43.6	39.4	60.8

cover indicate clearly that the sod of extensive tracts in the uplands should never have been broken. Likewise, the 14 to 42 percent in grass where the prevailing slope is greater than 10 percent indicates clearly the nature of the topography.

NATIVE VEGETATION

The mixed prairie of the Central Nebraska Dissected Loess Plains differs from the true prairie adjoining it on the east in many ways. An outstanding difference is the presence over the entire area of short grasses, predominantly blue grama, which cover the drier portions of the uplands in more or less pure stands, and alternate with mid and tall grasses, or form an understory beneath them (Figs. 16 and 17). Buffalo grass suffered heavy losses during the great drought (1933-40) and is now absent or occurs sparingly in many ungrazed tracts. This area of mixed prairie is further characterized by considerable amounts of plains muhly *(Muhlenbergia cuspidata)*, purple three-awn *(Aristida purpurea)*, and red three-awn *(A. longiseta)*, sand dropseed, and especially large amounts of western wheat grass. All of these grasses were rare in the true prairie eastward before the great drought (Weaver & Fitzpatrick 1934). Sand dropseed became very abundant in true prairie during the drought but is now largely displaced by more mesic grasses (Weaver & Bruner 1945). The eastward invasion of western

FIG. 16. A half section of ungrazed mixed prairie south of Litchfield. This unfenced prairie was adjacent to a large pasture on the right. The foreground is mostly blue grama with hairy chess. Trees in the background had been planted, but the homestead was abandoned long ago.

FIG. 17. Typical mixed prairie consisting of a lower layer of short grasses and an upper layer of a mid grass (western wheat grass).

FIG. 18. A common xeric forb of mixed prairie, narrow-leaved four-o'clock *(Allionia linearis)*.

FIG. 19. Plants of few-flowered psoralea *(Psoralea tenuiflora)*. This species is often abundant in both prairie and pasture.

wheat grass has resulted in profound changes in true prairie; it is disappearing only slowly (Weaver 1942, 1948). Conversely, several species of grasses abundant eastward were not found or were rare. Among these were prairie dropseed *(Sporobolus heterolepis)*, needle grass *(Stipa spartea)*, and slough grass *(Spartina pectinata)*.

This loess bluff area is also characterized by a large number of xeric western forbs which occur sparingly or not at all in the western margin of true prairie. The following are examples: *Sideranthus spinulosus, Malvastrum coccineum, Gaura coccinea, Chrysopsis villosa, Cirsium ochrocentrum, Allionia linearis, Solidago mollis, Geoprumnon plattense, Astragalus lotiflorus, Neomamillaria vivipara* (Nutt.) Britton & Rose, and *Thelesperma gracile* (Figs. 18, 19, and 20). Conversely, numerous species common on uplands of eastern Nebraska occur here only rarely or not at all. Among these the following are examples: *Helianthus rigidus, Euphorbia corollata, Liatris scariosa* Willd., *L. pycnostachya* Michx., *Coreopsis palmata, Meibomia canadensis, M. illinoensis, Baptisia bracteata*, and *B. leucantha*. *Psoralea tenuiflora* has replaced *P. floribunda*.

FIG. 20. Detail of red false mallow *(Malvastrum coccineum)*. This is the most drought resistant forb of mixed prairie. It occurs in greatest abundance intermixed with the short grasses.

COMMUNITIES OR TYPES OF PRAIRIE

Every considerable sample of the mixed prairie included four types. These were the short-grass, mid- and tall-grass, and western wheat grass communities, and a fourth type where the preceding were more or less intermixed. The short-grass type was most extensive, at least since the great drought, hence it is described first. The former mid-grass type has become considerably modified to a mid- and tall-grass community, especially since 1933, by the great spreading of big bluestem *(Andropogon furcatus)* following the heavy losses of little bluestem *(A. scoparius)*. On the whole, the mid-grass type has undoubtedly become restricted to much less than its former area. As to the extension of western wheat grass over great areas formerly occupied by other grasses, the evidence is overwhelming that this has occurred here just as it has taken place in the western portion of true prairie (Weaver & Albertson 1943).

SHORT-GRASS TYPE

The most important characteristic of this community was the fact that the short grasses dominated usually in almost pure stands or even where there was an intermixture of taller grasses such as side-oats grama *(Bouteloua curtipendula)*. A second characteristic of great importance was the fact that blue grama was far more abundant than buffalo grass. The latter was often entirely lacking or, if present, it nearly always occurred as a species of less importance in virgin, ungrazed prairie. In fact, its abundance was often a sign of disturbance at some previous time and, as will be shown, its amount where it was present increased with grazing until the result was a buffalo grass range. It was more apt to be found, at least in abundance, in prairies adjacent to old buffalo grass pastures than in large areas of well managed ranges.

Causes of the present greater abundance of blue grama were twofold. This species was harmed much less by severe drought, and, because it is a little taller, it endured shading caused by rank growth of vegetation much better than buffalo grass. Such luxuriant growth of both weeds and native plants occurred during 1942-47.

In the drier portions of most prairies there usually existed a rather dense sod-mat of blue grama or of this species intermixed with or sometimes alternating with rather extensive patches of buffalo grass. These sites usually included slopes where runoff was high but they were not necessarily those most exposed to sun and wind (Fig. 21). Many north-facing slopes or those facing east and north were carpeted more or less entirely with short grasses. Conversely, areas of short grasses even on dry south and southwest slopes were often divided into belts or patches by the presence of narrow to wide bands of mid grasses on catsteps. Mid grasses also occurred just below the upper borders of ravines where there was an accumulation of runoff water.

Location and extent of the short-grass type was

FIG. 21. Blue grama and buffalo grass on a hilltop where drought had opened the cover. The bare areas are not yet all reclaimed. Photo June, 1945.

FIG. 22. Portion of an extensive east-facing slope covered with blue grama overtopped by hairy chess. The prairie to the left consists largely of western wheat grass. Photo July, 1947.

usually set in sharp relief by the ever-present overtopping layer of the weedy annual, hairy chess *(Bromus commutatus)*. It was a well established invader that became abundant during the years of drought. The matured stand of short grass had foliage 4-8 inches tall but it was always overtopped by the panicles of hairy chess which dried in place and became almost white in mid and late summer (Fig. 22). Sometimes this brome alone occupied otherwise bare soil. In the alternes of mid and tall grasses (including western wheat grass) hairy chess often occurred, but even if abundant it was far less conspicuous because of its relatively lower stature. How long this brome will persist is unknown. It has greatly decreased and often entirely disappeared under the thick stands of mid grasses in true prairie.

Species of secondary importance intermixed with the short grasses included hairy grama *(Bouteloua hirsuta)*, purple three-awn, red three-awn, plains muhly, and sand dropseed in the more xeric category. Side-oats grama, June grass *(Koeleria cristata)*, and Scribner's panic grass *(Panicum scribnerianum)* formed an intermediate group, and big bluestem and nodding wild rye *(Elymus canadensis)* were chief among the taller grasses. An understanding of this phenomenon can be had only by considering the drought. Some of the steep ridges and driest slopes even today—after 6 or 7 years with good rainfall—are clothed chiefly with large bunches of blue grama so widely spaced that half of the soil is bare. During the 7-year drought, whole hillsides and even level hilltops were laid bare of vegetation or nearly so. It was at this time that the predrought dominant, little bluestem, largely disappeared. Much territory dominated by it and its associates was claimed during drought by short grasses, particularly blue grama, for this species was the most drought-enduring grass of all. During moist springs of certain years of drought this species flourished and spread widely. There was a gradual gain among short grasses (and also of western wheat grass) while most other species waned. Hence today many of the preceding relict grasses are intimately mixed with short grasses.

MID- AND TALL-GRASS TYPE

On the lower slopes of the hills and in the ravines, which mostly have broad flat bottoms, there are environments favorable for the development of mid- and tall-grass vegetation (Fig. 23). Many ravines have banks with slopes which reach a vertical distance of 10 to 25 feet above the level bottom. These are partially protected from wind and sun and in addition they receive much runoff water from the surrounding upland. Where the eroding valleys have cut far back into the bluffs, such places may occur not far from the hilltops. Typically there is no drainage ditch to interfere with the mowing of the vegetation for hay (Figs. 24 and 25). Locally such places are known as "hay pockets" since the yield is much greater than that on the bluffs.

FIG. 23. Community of mid and tall grasses in a flat-bottomed ravine where snow and runoff water from the slopes increased the water content of the soil. Note the bordering shrubs (right) on the north-facing slope.

Where the soil had slumped to produce catsteps on the hillsides, vegetation was of much the same type as in the valleys and ravines (Fig. 26). Here the relict little bluestem, usually scattered but sometimes dense locally, represented the remnants of the former stands of this predrought dominant. But big bluestem was the chief dominant in all such places as it was also in streaks and patches on moist, protected hillsides.

The sod-forming big bluestem had spread widely and often thickened its stand to the exclusion of both

FIG. 24. Big bluestem (dark), Indian grass *(Sorghastrum nutans)*, and mid grasses on the floor and sides of a shallow ravine near Amherst in August, 1947.

FIG. 25. A native prairie mowed for hay in August, 1947. It is about 27 miles north of Elm Creek. Prairie grasses remain undisturbed on the banks that are too steep for mowing. Some banks (left) are covered with shrubs.

FIG. 26. Prairie 15 miles southeast of Broken Bow showing catsteps on the steep banks of a ravine (left) and on the hillside in the distance. Here the mid- and tall-grass type of prairie prevails. Relict little bluestem was common.

short and mid grasses. Nodding wild rye was common here and there in these moist areas as was also switchgrass *(Panicum virgatum)*, especially in the valleys. A stand of switchgrass indicated the best water supply. Nodding wild rye was found in greatest abundance where disturbance had occurred, as by the deposit of soil in a ravine. Indian grass *(Sorghastrum nutans)* was usually not abundant and slough grass was rarely found. Several coarse carices as *Carex gravida*, *C. brevior* (Dewey) Mackenzie, and others, were often more or less plentiful. Postclimax tall grasses sometimes occurred, each in pure stands, but often they were intermixed. Kentucky bluegrass *(Poa pratensis)* intermingled with nearly all of them. In this type, short grasses were practically excluded.

On the sides of the ravine above the reach of the mower, the mulch of dead big bluestem was often 5 to 10 inches deep, since the prairie was rarely burned intentionally. In this debris, which was sometimes more than a foot deep, one could readily distinguish three crops of dead plants—two of decaying leaves and one of leaf mold—under the living grasses. This accumulation of material prevented the development of an understory, greatly delayed development in spring, and thinned the new stand of big bluestem or other tall grasses to about one-third the usual number of stems.

The second most abundant grass was side-oats grama. It occurred widely and often in nearly pure stands on the catsteps and banks above the steep slopes of the ravines, or in patches in the valleys (Fig. 27). Like the other mid grasses it alternated with the rankly developed tall grasses or intermingled with them. June grass, plains muhly, and tall dropseed *(Sporobolus asper)* were of common occurrence.

FIG. 27. A nearly pure stand of side-oats grama on a steep slope near a ravine. Small amounts of hairy chess are intermixed.

Relict needle grass was rarely found. Kentucky bluegrass was often well represented in the understory as were also Scribner's panic grass, Wilcox's panic grass *(Panicum wilcoxianum)*, and penn sedge *(Carex pennsylvanica)*. Bluegrass, as in true prairie, had made enormous gains during a wet cycle following the drought. It was not uncommon to find it in almost pure patches in ravines and on normally dry slopes growing side by side with blue grama. It was commonly intermixed with various mid grasses. The two smaller panic grasses often occurred in pure stands in small patches formed during drought. Patches of western wheat grass were common and

indeed abundant where this drought-evading species had replaced the other grasses. Where the cover was open, sand dropssed was frequently found. Hairy chess occurred more or less abundantly, being thinner or absent where the shade was denser. It was thickest where damage by drought was greatest. In small patches it still constituted practically the only vegetation.

Mixed Short and Taller Grasses

In addition to the short-grass type and the much more mesic one composed of tall and mid grasses, there were transitional areas of considerable extent where species from the two types grew more or less in equal abundance, forming the characteristic layered vegetation of mixed prairie. Big bluestem with an understory of blue grama, and less often buffalo grass, was a product of the drought (Fig. 28). When the formerly abundant little bluestem largely succumbed, big bluestem, intermixed with it, often survived, partly because of its deeper root system but often because of its rhizomes. These are known with certainty to have remained dormant 5 to 7 years both in true prairie and in mixed prairie (Weaver & Albertson 1944, Weaver & Bruner 1945). During the least severe of the years of drought much big bluestem spread widely. This spreading was accelerated when the rains finally came and the thin stands thickened greatly. Likewise the short grasses invaded much territory formerly occupied mostly by little bluestem but also by smaller amounts of big bluestem. This also resulted in the apparent anomaly of the short grasses forming an understory to the postclimax big bluestem in many sites.

Fig. 28. A square mile of mixed prairie about 10 miles southwest of Ansley, showing belts and streaks of big bluestem (dark), frequently with an understory of blue grama. The lighter colored portions are hairy chess intermixed with short grasses and several species of mid grasses. Photo August, 1947.

Side-oats grama developed vigorously, produced abundant seed crops, and spread very widely during drought, when released from severe competition of other grasses. It was intermingled with the short grasses over vast areas. Sand dropseed was still abundant in the driest situations along with the short grasses but it was much less abundant than side-oats grama. Some relict little bluestem, rapidly increasing in amount, was intermixed with the short grasses. Purple three-awn, plains muhly, June grass, and bluegrass taken together sometimes bulked large. Often there was about an equal mixture of mid grass overtopping the short grass.

Areas in true prairie where whole hillsides were almost bared of vegetation by drought were repopulated by half a dozen dominant species in about equal numbers. They formed a complete cover, but not enough time had elapsed for the usual prairie types to develop. This was also true in considerable portions of mixed prairie. The vegetation was simply a mixture of all the grasses that chanced to survive or migrate quickly while there was room for all. These unstable communities are best described as merely a mixture of grasses. They did not occur before the catastrophe of great drought.

Western Wheat Grass Type

The extensive spreading of western wheat grass during the period of drought has been remarkable. In true prairie eastward it made a phenomenal increase from a species of very minor importance to one of first rank. "Immediately after 1934, it became increasingly abundant in true prairies and native pastures. It has continued its spread over all types of terrain wherever bared places or open stands of other grasses had resulted from the terrible drought" (Weaver & Albertson 1943). Western wheat grass was found in greater or lesser amounts in every prairie examined. Since dust deposits often aided considerably in its invasions, it was usually very abundant where prairie was adjacent to cultivated land. In amount it varied from almost complete replacement or overtopping of other vegetation, through extensive alternes in short grass or other prairie grasses, to patches so small or stands so thin that they had little effect upon the prairie cover as a whole. Moreover, distribution had no relation to type of soil, slope, or exposure. It was found on valley floors, on both gentle and steep slopes, and on hill crests and catsteps. Amount and extent were entirely unpredictable, but were probably related to such factors as direction and velocity of wind, bareness of slopes, and abundance of seed supply. It rarely if ever replaced established vegetation. Its distribution and abundance may best be explained by a few examples.

About 10 miles northeast of Hazard there occurs a quarter section of nearly level land except for several deep ravines which have worked half way across the tract from the east side. The unbroken eastern half, which had been clothed with a cover of mid and short grasses, had become, by July 1947, a sea of dense western wheat grass with foliage nearly 2 feet high and abundant spike-topped flower stalks 3 feet tall. Great dust storms and drought had resulted in the death of practically all of the former vegetation. The area closely resembled a field of ripening grain. It differed, however, in an almost continuous understory of hairy chess, 15 inches high, and an intermittent lower layer of *Ionoxalis violacea.*

Forbs were few and entirely confined to *Solidago mollis, Lygodesmia juncea,* and other species of great drought resistance. Only rarely was a small "island" of blue grama seen.

A much smaller portion of the area differed only in that an understory of blue grama occurred beneath the western wheat grass. Although western wheat grass also completely clothed the banks and bottoms of some ravines, the original communities of tall grasses and mid grasses remained intact and were flourishing elsewhere. All the prairie grasses usually found in such sites were plentiful and in addition a wealth of lowland and upland forbs remained. This presented a striking contrast to the monotonous cover of western wheat grass. The only other vegetation was thickets of shrubs and vines. A similar prairie of western wheat grass is shown in Figure 29.

FIG. 29. Prairie 15 miles west of Loup City where the chief dominant everywhere is western wheat grass. Aside from patches of buckbrush *(Symphoricarpos occidentalis)*, even the ravine is covered with this grass.

Another example of the invasion of western wheat grass was shown on a grand scale in a prairie approximately 15 miles southeast of Broken Bow. This whole range of 160 acres, except an east-facing slope, had been taken over by western wheat grass (Fig. 22). Drought had been prolonged and intense, for over much of this part the relict blue grama occurred only in widely spaced bunches. There was a continuous cover of hairy chess in which there were many species common under great disturbance, as six-weeks fescue *(Festuca octoflora hirtella)*, little barley *(Hordeum pusillum)*, horseweed *(Leptilon canadense)*. Pursh's plantain *(Plantago purshii)*, and sand dropseed. Drought-formed patches of penn sedge, Scribner's panic grass, and involute-leaved sedge (*Carex eleocharis* Bailey) were present, but no buffalo grass. The cover varied from nearly bare soil to 75 percent blue grama. Relict little bluestem occurred plentifully along the catsteps in stands 80 percent pure near the very tops of the high hills (Fig. 26). The little bluestem type must have extended far down the slopes, since the invading western wheat grass had no understory of relict blue grama. There was only a dense stand of wheat grass with an abundance of hairy chess. Forbs likewise had practically disappeared. This seemed due to the deposition of a layer of dust from fields to the south and west. Great bunches of relict blue grama crowned the tops of the hills. Here also relict needle-and-thread *(Stipa comata)* grew thickly. The mid grasses on the uninvaded catsteps, wherever they occurred, grew luxuriantly and were intermixed with numerous prairie forbs.

A few miles west of Ord, a quarter section of mixed prairie was examined. It is described here because of the vivid manner in which it portrayed the mosaic of vegetation resulting from dust and drought. The topography was rough, steep hills being separated by deep ravines. Over much of the area western wheat grass had replaced most of the former vegetation. Description of the cover is that on a long hill running west of north and bounded on all sides except the north by deep ravines (Fig. 30).

FIG. 30. View looking southeast from the top of a long hill several miles west of Ord. The deep east-west ravine separating this bluff from the one nearer the road with a single small patch of western wheat grass is obscured by the base of the hill. Note cultivated fields of maize on this rolling land. August, 1943.

The main axis was ¼ mile long. The south face was steep and much smaller than the very extensive east and west slopes.

Upon crossing the main ravine from the south one entered a continuous belt of almost pure western wheat grass on the nearly level lower part of the slope. This phenomenon of the death and replacement of big bluestem and its associates was rather common on such highly insolated areas where run-in water was normally plentiful in the lowland soil. The tall grasses had evidently not been rooted deeply enough to withstand extreme drought (Weaver & Albertson 1943). Western wheat grass swept around the base of the hill both eastward and westward in a belt only a few yards wide. On the lower slope proper, there occurred a zone of big bluestem.

The bluestem vegetation, formerly continuous across the ravine, extended upward on south and east slopes above the western wheat grass for a few yards

only. The foliage was 3 feet high and flower stalks were 6 feet tall. Examination made it clear that this grass had now rooted more deeply than formerly. Side-oats grama, growing with the bluestem, put forth flower stalks to the unusual height of 40 inches, thus giving evidence of the presence of abundant moisture.

Side-oats grama formed a distinct belt from a few to many yards wide on the upper banks where the more gentle slope of the hilltop gave way abruptly to a precipitous one. Here runoff was normally high and much erosion occurred. This grass either withstood the terrible drought which swept the hill almost free of vegetation, or reseeded quickly from large relict bunches with the coming of favorable seasons. Actually both phenomena had occurred.

The long southwest slope, the hill top, and the east slope had practically lost their cover of mid and short grass during the early years of drought (1934-36). They were now a field of western wheat grass. An exception was a narrow belt of mixed big bluestem and side-oats grama fringing the east ravine. But across this ravine, western wheat grass recurred and swept over the adjacent hill and down to the next valley. Not only were all of the former grasses replaced but also all of the forbs, except a few of the most drought resistant, had succumbed.

The distribution of western wheat grass was not at all uniform in amount in different samples of prairie. Sometimes only a little was present. It often covered a single ridge or only a particular slope, or small patches only occurred in a ravine. Oftentimes a thin overstory was found or possibly a few dense patches. But not a single prairie was examined where western wheat grass was entirely absent. Streaks and patches, pure or intermixed with short grass or mid grass, were the rule where formed an upper story to the short grasses over more extensive invasion had not occurred. It probably area than any other species.

The several communities of the prairie vegetation have been described separately only for the purpose of clarity. The boundaries were often indefinite and fragments of one community frequently occurred as patches or islands in the others. The vegetation had undergone great changes due to drought and dusting and was in a stage of rapid recovery. Such stability as occurs between the longer cycles of severe drought has not yet been attained.

Résumé of Grasses

The grasses and sedges of the mixed prairie in this loess bluff region occurred in the following groups:

Dominant Species

Short-Grass Type (Faciation)

Bouteloua gracilis	*Buchloe dactyloides*

Mid- and Tall-Grass Type (Postclimax associes)

Andropogon furcatus	*Panicum virgatum*
Bouteloua curtipendula	*Elymus canadensis*
Agropyron smithii	

Mixed Short and Taller Grasses (Typical expression of association)

Andropogon furcatus	*Bouteloua gracilis*
Bouteloua curtipendula	*Buchloe dactyloides*
Agropyron smithii	

Western Wheat Grass Type (Consociation)

Agropyron smithii

Species of Secondary Importance

(Of greater abundance)	(Of lesser abundance)
Muhlenbergia cuspidata	*Panicum wilcoxianum*
Poa pratensis	*Aristida purpurea*
Koeleria cristata	*Aristida longiseta*
Sporobolus cryptandrus	*Carex eleocharis*
Panicum scribnerianum	*Sorghastrum nutans*
Carex pennsylvanica	*Bouteloua hirsuta*
Sporobolus asper	*Schedonnardus paniculatus*
Andropogon scoparius	*Stipa comata*
	Stipa spartea

Hairy chess, as previously stated, was present to very abundant in every place where soil was exposed in sufficient amounts so that the seed could find lodgement and germinate, and where the seedlings were not completely suppressed by dense shade. This annual is a drought invader and not a permanent part of the vegetation. It is a seral dominant.

Forbs

The great injury to grassland by drought and burial by dust was shown by the effect upon the population of forbs. Near the end of the drought the number of species generally distributed were few and most forbs had succumbed, were dormant, or were confined to the most protected sites. But during the several years following the drought nearly all reappeared from seed or dormant underground parts (Fig. 31). Their approximate importance is indicated in the following lists:

Principal Species of Forbs

Amorpha canescens	*Lygodesmia juncea*
Aster multiflorus	*Malvastrum coccineum*
Callirhoe involucrata	*Petalostemum purpureum*
Cathartolinum rigidum	*Psoralea argophylla*
Cirsium undulatum	*Psoralea tenuiflora*
Echinacea pallida	*Ratibida columnaris*
Gaura coccinea	*Rosa pratincola G.*
Geoprumnon crassicarpum	*Sideranthus spinulosus*
Geoprumnon plattense	*Solidago glaberrima*
Ionoxalis violacea	*Solidago mollis*
Kuhnia glutinosa	*Toxicodendron rydbergii* (Small) Greene
Liatris punctata Hook.	
Lithospermum linearifolium	

Forbs of Secondary Importance

Acerates auriculata	*Cirsium ochrocentrum*
Agoseris cuspidata	*Cogswellia daucifolia*
Allionia linearis	*Cogswellia orientalis*
Allium mutabile	*Delphinium virescens*
Allium nuttallii	*Drymocallis agrimonioides*
Ambrosia psilostachya	*Erigeron ramosus*
Anemone caroliniana	*Gaura parviflora*
Antennaria campestris	*Glycyrrhiza lepidota*
Artemisia gnaphalodes	*Hedeoma hispida*
Asclepias pumila	*Hosackia americana*
Asclepias verticillata	*Lathyrus ornatus*
Aster oblongifolius	*Meriolix serrulata*
Astragalus lotiflorus	*Morongia uncinata*
Astragalus shortianus	*Nabalus asper*
Cathartolinum sulcatum	*Neomamillaria vivipara*

Oenothera biennis
Onosmodium occidentale
Opuntia humifusa
Oxytropis lamberti
Parosela enneandra
Pentstemon albidus
Petalostemum candidum
Physalis heterophylla
Physalis lanceolata
Plantago purshii
Polygala verticillata
Psoralea esculenta
Senecio plattensis
Solidago altissima
Strophostyles pauciflora
Thelesperma gracile
Tradescantia bracteata
Vernonia baldwinii
Vicia americana
Vicia sparsifolia
Xanthoxalis stricta

FIG. 31. Two common forbs of mixed prairie; wavy-leaved thistle *(Cirsium undulatum)* left, and lead-plant *(Amorpha canescens)* right. Both spread by underground parts.

One of the most abundant, conspicuous, and widely distributed plants was the lead-plant *(Amorpha canescens)* (Fig. 32). Although it is a half-shrub it behaves as a forb under annual mowing. In abundance, it is an excellent indicator of grassland that has been ungrazed for a long time. It had increased greatly since the sod was opened by drought, and was often abundant in the short-grass type. Two other species which were not found so regularly but locally had increased enormously were the buffalo bean *(Geoprumnon crassicarpum)* and *G. plattense.* In numerous places single plants of buffalo bean were 3 to 4 feet in diameter (Fig. 33). Like aggregated mats of *G. plattense,* they grew so closely together that the soil was covered almost continuously over many square yards. Many other principal species of forbs as *Callirhoe involucrata, Kuhnia glutinosa, Ratibida columnaris, Solidago glaberrima, S. mollis,* and *Psoralea tenuiflora* formed societies of much greater density than the writers have ever before observed. This great increase in numbers of certain forbs was balanced by fewer numbers and greater localization of many others. *Gaura coccinea, Sideranthus spinulosus* and *Lygodesmia juncea* were representative of numerous other species which were found rather regularly but ordinarily in about their predrought abundance. Wherever western wheat grass occurred forbs were invariably few. This resulted from the use of water by the grass even to depths of 6 to 8 feet early in spring. The soil became dry and later awakening species often succumbed to the drought (Weaver 1942).

FIG. 32. Typical thick society of lead-plant in a mixed prairie area about five miles west of Loup City. Side-oats grama is the dominant; there is also much hairy chess.

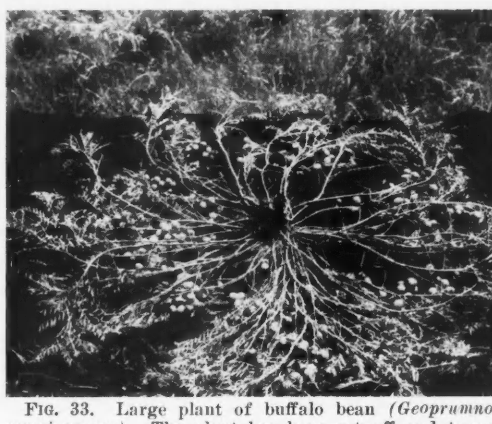

FIG. 33. Large plant of buffalo bean *(Geoprumnon crassicarpum).* The plant has been cut off and turned over to show the abundant fruits. The spread of this plant is about 4 feet.

SHRUBS

The story of the distribution of the vegetation would be incomplete if the shrubs, vines, and small trees were overlooked. On the north-facing slopes especially, but also on others partially protected from wind and sun, there often occurred fringing thickets of shrubbery (Fig. 23). For here, in addition to the rainfall, water runs in from the slopes above, and wind-blown snow accumulates. The shrubs were sometimes more or less intermixed with the tall grasses, but where they were well developed the grasses largely or entirely disappeared. These postclimax thickets consisted chiefly of buckbrush

(Symphoricarpos occidentalis), choke cherry *(Prunus melanocarpa)*, wild plum *(P. americana)*, and smooth sumac *(Rhus glabra)*. Buckbrush often formed thickets on the valley floor as well, but its spread was usually held in check by annual mowing. Often the brush was 3 feet tall and so dense that even bluegrass was shaded out. Similar dense copses of the other species which grow much taller (10 to 15 feet) were almost without undergrowth. Other shrubs were golden currant (*Ribes aureum* Pursh), gooseberry (*Ribes gracile* Michx.), poison ivy *(Toxicodendron rydbergii)*, and lead-plant, which reached a height of 3 to 4 feet. The prairie rose *(Rosa pratincola)* was represented by large bushes, and fox grape *(Vitis vulpina)* climbed over the shrubs. Sometimes small trees of white elm *(Ulmus americana)* occurred or those of boxelder *(Acer negundo)* and ash *(Fraxinus pennsylvanica)*, but trees were more commonly found only along streams. Various mesic herbs as *Helianthus tuberosus*, *Monarda mollis*, and others not mentioned in the list of prairie forbs also occurred here.

PASTURES

This great tract of mixed prairie has been used chiefly for grazing. Considerable areas have retained their native cover, except that it is annually mowed for hay that is fed to livestock in winter. But by far the larger part is used for summer range, chiefly for cattle. Livestock is sustained by the range grasses from spring until late fall, and sometimes parts of the pastures are used only for winter grazing. Under continued grazing there are many changes in the composition of the vegetation even under good range management, and much degeneration of the grassland occurs under close grazing and trampling (Weaver & Hansen 1941).

Early Survey

A survey of many ranges in the northern and western portions of the area was made in 1943, about 2 years after the great drought. The ranges varied in size from 80 acres to a square mile or more (Fig. 34). These mixed-prairie pastures consisted chiefly of blue grama although buffalo grass was found in moderate amounts, and it was abundant in old, closely grazed pastures (Fig. 35). Big bluestem was the chief tall grass; side-oats grama was of much less abundance except on the catsteps and steep banks. Western wheat grass occurred sparingly to abundantly, having populated many drought-bared or dusted areas regardless of slope or topography. In general, the ranges were not overgrazed, in fact most were moderately utilized, and some had not been pastured or at least had been grazed only intermittently since the great drought. For then herds of cattle were depleted and they had not been built up again.

The drought (and sometimes burial by dust) had left its marks of destruction almost everywhere, except perhaps on portions of well protected north-facing slopes. Excessive grazing also had sometimes played a part in weakening the grasses before

Fig. 34. Broad expanse of range land, looking north from a hilltop in the Sheen pasture near Kearney.

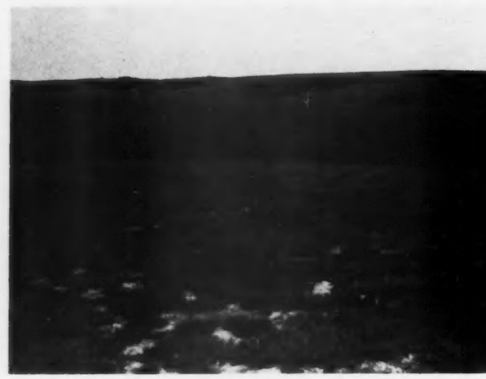

Fig. 35. Prairie reduced to short-grass pasture. Only in the ravines, which erode laterally, and up their steep sides were many relict mid grasses found.

drought occurred. Although a few greatly damaged ranges were still in the early or medial stages of a subsere, most of them were well on the way toward the reestablishment of a short-grass cover. The weedy stages had been succeeded by those of perennial grasses—often sand dropseed or western wheat grass—but mostly by blue grama.

In numerous places near the periphery of the main range area, pastures had not only been heavily grazed but also subjected to considerable dusting from cultivated fields. The hilltops and slopes had been nearly bared, except for relict bunches and patches of blue grama and remnants of buffalo grass in the most sheltered places. The buffalo grass returned quickly after 1940 and had occupied most of the area; even the hilltops and ridges were again two-thirds covered. Relict plants and small patches of big bluestem, little bluestem, side-oats grama and a few other mid grasses were common on the protected banks (Fig. 36). Where the dust was deep, patches and streaks of ruderals occurred.

In most ranges the cover had been greatly disturbed by drought. Even on north-facing slopes drought or dust coverage had been so severe that considerable amounts of western wheat grass grew

FIG. 36. Eroding soil where the hillside slopes give way to the steep banks which border the ravines. Note the good cover both in the ravine and on the hillsides. The light colored vegetation is a society of silvery psoralea *(Psoralea argophylla)*.

in patches and alternes. Blue grama had reestablished a fairly good cover elsewhere; buffalo grass was present mostly on the level upland though only in small amounts. The basal cover of the short grasses was frequently only 50 percent. Relict sand dropseed was common, sometimes in alternes; purple three-awn occurred on bared slopes, and dried and lodged downy brome *(Bromus tectorum)* and hairy chess formed an excellent mulch in some local, half-bared places. There were few weeds. Only relicts of earlier subsere species remained. Lower slopes near deep ravines were well clothed with both big blustem and little bluestem below the usual distinct belt of side-oats grama on the sharp break from hill to ravine. This distribution of vegetation on hilltops, slopes, and ravines was repeated again and again in various ranges.

The ranges on the loess hills in the vicinity of Broken Bow were so similar (except those greatly overgrazed) that a single description will suffice (Fig. 37). They were dominated by blue grama; buffalo grass, where present, occurred in small amounts. The cover had been greatly depleted by drought since the normal precipitation of 23.1 inches decreased to 13.1, 16.0, and 17.9 inches in 1934, 1936, and 1939, respectively. Since there occurs here a rather large and almost continuous area of range land, dusting had been at a minimum.

Because of the rugged topography, there were many protected slopes and ravines in which the mid and tall grasses were thriving and frequently dominating to the exclusion of short grasses. These occurred even on southern exposures provided there was enough run-in water. Chief among these grasses were big bluestem, side-oats grama, little bluestem, nodding wild rye, and switchgrass. But the extent of the lowlands and ravines dominated by this tallgrass community had been greatly reduced by the drought. The less mesic portions had been repopulated by mid and short grasses. Side-oats grama, which is the most xeric of the preceding species, had usually not played its important role as in true prairie in reclaiming drought-bared soil. Where the

FIG. 37. A hillside on loess bluffs between Broken Bow and Lexington. This is a small part of a range several hundred acres in extent.

ravines had broad flat bottoms and were well grazed, the cover was short grass, mostly blue grama. Weeds were not abundant. In general the succession following drought was in the late stage and approaching such stability as is maintained under grazing.

Growth of seedlings and best development of blue grama by tillers had often been retarded by an accumulation of debris resulting from light stocking or complete protection. Where alternes of wheat grass occurred they were scarcely grazed or entirely neglected by stock if other forage was plentiful. Sometimes the deep debris from the growth of two or more seasons' crops had accumulated and hindered rapid succession (Fig. 38).

In these ranges, June grass, plains muhly, purple three-awn, hairy grama, and tall dropseed were all found but usually in small amounts and they were never abundant, except locally. Needle grass was rare. Plains muhly had generally increased during the drought but red three-awn and purple three-awn were now recovering from nearly complete extinction. Tumble grass *(Schedonnardus paniculatus)* was a common indicator of disturbance. Its dried panicles lightened the hillsides where the cover of blue grama had been well opened by drought.

FIG. 38. A north slope covered with a dense stand of western wheat grass. Vegetation of preceding years is lodged here and forms a deep mulch. Unlike the rest of the pasture, this portion was entirely ungrazed.

Usually the soil between the bunches of blue grama was bare and cracked during summer drought, and in only a few ranges was there the usual cover of litter. This, of course, was an after-drought effect from which the vegetation had not yet recovered.

Excellent examples were observed of ranges that had gone far toward recovery from drought but were having the annual yield removed too close to the soil. Except in ravines there were neither native forbs nor weeds, since all vegetation except the wavy-leaved thistle *(Cirsium undulatum)* had been closely grazed (Fig. 39). Scarcely a single flower stalk of blue grama, which composed 85 percent of the grass, was found. The soil was, of course, barest on the hilltops. Here the basal cover often varied between 5 and 25 percent. Such close grazing is a dangerous prelude to deterioration or to desiccation. Grasslands that suffered most from drought were those formerly overgrazed. Just as desiccation affects vegetation first by decreasing the yield and then by reducing the basal cover, so too, close grazing is a first step in weakening underground parts, destroying seedlings, and inhibiting normal vegetative increase and the production of the necessary litter for protecting the soil (Weaver & Darland 1947).

Several features of these ranges may be emphasized in contrasting them with similar ones in mixed prairie occurring 50 to 200 miles southward and extending from Nebraska to Central Kansas (Albertson & Weaver 1942). A notable feature was the general thinning and opening of the cover of vegetation. Although this loess bluff area was not thoroughly studied in early drought, there is abundant evidence that while drought damage was great, it was not as serious as that in southern Nebraska and Kansas. Dusting was certainly far less, and recovery was somewhat more rapid, especially considering the small part played by buffalo grass in these steep loess hills. Under protection or moderate grazing the weed stages had disappeared.

The relatively few species of really abundant range grasses was a phenomenon characteristic of both

FIG. 39. Greatly overgrazed range near Ord. Almost the entire crop of forage had been harvested by the cattle and horses. The cover consists chiefly of blue grama. Photo July, 1943.

areas. On uplands blue grama played the major role here; buffalo grass and blue grama were of nearly equal importance southward. In fact, except for sand dropseed, they were often the only perennial grasses (Weaver & Albertson 1940). Because of the diversity of habitats, tall grasses (and especially big bluestem) were much more abundant here and the area dominated by postclimax species generally was much greater than that southward. Western wheat grass was also far more abundant.

Simplification of the structure of the vegetation had previously occurred as a result of long, continuous grazing. It resulted from the more or less complete removal of the mid-grass layer above the short grasses. Structure was further simplified by the almost complete removal by drought of many species of the ground layer and a wider spacing of the remaining ones. While forbs were still relatively few over the loess hills, species were far more abundant and numbers of individuals larger than southwestward. The number of species from true prairie was also much greater. All of these differences may be attributed to a combination of factors—topography, mellow and deep loess soils, and farther removal from the great central area of desiccation in the southwest.

LATER SURVEY

Under grazing, the tall and mid grasses are reduced in vigor much more rapidly than are the short grasses. This is largely due to the fact that more foliage is left on the shorter grasses when the range is closely grazed. Except on steep banks, the taller grasses occurred most abundantly on the level lowlands and lower slopes. Here these species, all of high palatability, were easily available to livestock and the impact of grazing was often heavy. The new growth of the bluestems and other plants was highly relished and they were soon regrazed. The livestock not only grazed in the bottoms of the ravines and in broad hay pockets often found in them, but also they were enticed by the lush forage to graze on the banks as well. Hence, even on the steep banks paths occurred which commonly ascended very gradually along the long axis of the slope. Indeed series of such parallel paths, 8 or 9 in number and one above the other, were common in older pastures where the banks of the ravines were high. By this means all of the forage on the entire slope had been reached. Even after the more or less level bottoms had degenerated into a vegetation of short grass, but not infrequently (in recent years) containing much bluegrass, the less accessible slopes often maintained much of their original cover. But in many ranges that had been heavily stocked, these banks, like the catsteps in other portions of the pasture, finally lost their tall and mid grasses because of grazing and trampling and became more or less completely clothed with blue grama, or with western wheat grass and buffalo grass (Fig. 40). The valley below was often clothed with short grass or western wheat grass except where enough eroded soil had been deposited to maintain a weedy subsere.

FIG. 40. View in an old buffalo grass pasture near Ravenna showing mats of buffalo grass on the rough banks of a ravine which have entirely replaced side-oats grama and other mid and tall grasses usually found in such places. Chief weeds are ironweed *(Vernonia baldwinii)* and hoary vervain *(Verbena stricta)*.

On the lower slopes of hills and on the catsteps, wherever they occurred, the gradual degeneration of tall and mid grasses had been similar, although relicts often persisted a long time. Where mixed short and taller grasses grew, all but the short grasses were ultimately "grazed out."

A second area where grazing was usually heavy was on the more or less level hilltops and upper slopes. Consequently the grasses here were often less vigorous when drought came and the losses were far greater than on midslopes where grazing had been less severe.

The general effects of drought on the range was to decrease the amount of buffalo grass much more than that of the more drought resistant blue grama. Where these two grasses occurred in mixture it was not uncommon for buffalo grass to entirely disappear from the ridges, which were then reclothed from the relict clumps of blue grama. In many pastures the blue grama had succeeded in covering only a fourth or a third of the soil of the ridges and steepest slopes. On other hilltops the interspaces had only begun to be filled with patches of buffalo grass.

Long continued heavy grazing of a mixture of short grasses was less harmful to the sod-forming buffalo grass than it was to the bunches of blue grama. Hence such ranges suffered great denudation during drought, but they also recovered more quickly after drought, the soil being rapidly reclaimed by stolons of relict plants and patches of plants of buffalo grass or by means of their seedlings. While many ranges had at least relict patches of big bluestem, side-oats grama, and little bluestem—since these taller grasses persisted a long time—in the main (except for western wheat grass) they were short grass pastures. This is revealed in Table 6.

In Table 6 the general location of each of the 29 pastures is indicated only approximately by one of the nearest towns. The grazing intensity is that of the current year. This had nearly always been the same the preceding year. The basal area is the average of estimates over the portion of the range dominated by short grasses. This type nearly always occupied all but small portions of the range. Exceptions were areas of wheat grass, and rarely sand dropseed, on certain slopes with extensive catsteps. The percentage composition of the cover is that of the dominant species only; the small amounts of various other grasses and forbs were not considered. Annuals as little barley and hairy chess are discussed elsewhere.

Of the 29 pastures listed in Table 6, 9 were characterized by buffalo grass (with only 15 percent or less of blue grama) and 8 by blue grama (with buffalo grass 15 percent or less in abundance). But where larger percentages of the second ranking grass were present, buffalo grass exceeded blue grama in only 3 pastures, while blue grama exceeded buffalo grass in 7. Grazing was light, moderate, or none in 18 of the pastures, 9 were overgrazed, and 2 were intermediate. The first 13 in the table were studied in 1943, and the remainder in 1946 and 1947. It should be emphasized that nearly all of the buffalo grass pastures were near the periphery of extensive grazing areas, where much of the land was farmed. The ranges were smaller and grazing nearly always more intense. This was also true in a large measure in all ranges where the percentage of buffalo grass exceeded that of blue grama.

A few facts about some of the grasses previously mentioned should be added, and the occurrence of other species pointed out. The distribution of western wheat grass was difficult to describe. It was of no importance in some pastures, in others it was scattered lightly nearly throughout; sometimes there were dense local patches only, but in still others there were extensive stands. Furthermore, while western wheat grass sometimes dominated almost to the exclusion of other grasses, more usually it formed an overstory to the short grasses; but it was also intermixed with side-oats grama, big bluestem, or sand dropseed, and less frequently with other species.

Side-oats grama, aside from western wheat grass, was probably the most widely distributed mid grass. In moderately grazed pastures it occurred thinly, or locally thickly, from hilltop to ravine bottom. When finally replaced by a dense sod of short grasses, relicts still occurred along the banks of ravines and on catsteps. Since the years of above-normal precipitation, some Kentucky bluegrass has been present in nearly every pasture. Always grazed closely, it was often found in small to extensive patches in the bottoms of ravines. Sometimes it had spread upward along ravines to hilltops, and it was also found with mid grasses on the catsteps.

The abundance of sand dropseed in the subsere during drought, where it not infrequently dominated in pure stands, has been mentioned. It was scattered here and there among other grasses but also occurred in abundance from the steepest hillcrests to the denuded soil in eroding bottoms of ravines or on their banks. Bared or semibared areas, whether due to

TABLE 6. General location, type, and grazing intensity of 29 representative pastures in the loess bluffs. Variation in the basal cover from the average of the more open to the average of the denser short-grass type is shown in percent. The estimated percentage composition provided by each of the dominants is included and the general condition in regard to weeds.

Station	Type	Grazing intensity	Basal cover, percent	Composition perennial grass cover, percent		Weeds
West of Ravenna	Buffalo grass	Moderate	80-98	Bda[1] 80	Bgr 19	Few
Northwest, Ravenna	Buffalo grass	Moderate	25-100	Bda 85	Bgr 13	Many
South of Loup City	Blue grama	Light	50-60	Bgr 80	Bda 5	Few
West of Loup City	Sand dropseed	Ungrazed	75-85	Scr 95	Bgr 5	Few
South of Broken Bow	Blue grama	Moderate	35-40	Bgr 80	Asm 12	Few
Southeast, Broken Bow	Blue grama—buffalo grass	Overgrazed	5-8	Bgr 95	Bda 5	Many
East of Broken Bow	Blue grama	Light	35-40	Bgr 85	Asm 8 Bda 5	Few
North of Broken Bow	Blue grama	Light	30-40	Bgr 90	Asm 5	Few
East of Round Valley	Blue grama—buffalo grass	Light	50-95	Bgr 60	Bda 35	Few
West of Ord	Blue grama	Overgrazed	40-50	Bgr 85	Bda 15	Few
Southeast of Ord	Wheat grass—side-oats grama	Ungrazed	....	Asm Bcu	Afu	Few
Near North Loup	Blue grama—buffalo grass	Ungrazed	40-60	Bgr 60 Scr 15	Bda 20	Few
West of Greeley	Blue grama—side-oats grama	Overgrazed	5-80	Bgr 70	Bcu 25	Many
Northwest of Kearney	Buffalo grass—blue grama	Moderate	80-85	Bda 75	Bgr 25	Many
Miller	Buffalo grass—blue grama	Moderate	80-85	Bda 66	Bgr 33	Many
Northeast, Lexington	Blue grama—buffalo grass	Moderate to close	50-80	Bgr 60	Bda 40	Few
Cumro	Blue grama	Moderate to close	30-75	Bgr 85	Bda 15	Many
North of Elm Creek	Buffalo grass	Ungrazed	80-90	Bda 90	Bgr 10	Many
Poole	Buffalo grass	Moderate	80-90	Bda 90	Bgr 1	Many
Northwest of Ravenna	Blue grama—buffalo grass	Overgrazed	30-40	Bgr 60	Bda 40	Many
Northeast, Mason City	Blue grama	Overgrazed	40-80	Bgr 60	Bda 40	Few
Southeast, Broken Bow	Buffalo grass	Overgrazed	20-40	Bda 85	Bgr 10	Many
West of Buckeye	Blue grama	Moderate	50-60	Bgr 95 Bda 5 (slopes) Bda 0-80 (flat uplands)		Few
South of Ansley	Blue grama—buffalo grass	Moderate	60-90	Bgr 50 Bgr most widespread	Bda 50	Few
South of Berwyn	Blue grama—buffalo grass	Moderate	60-70	Bgr 50-95	Bda 20-50	Many
West of Kearney	Buffalo grass	Overgrazed	75-80	Bda 80	Bgr 10	Few
Northwest of Kearney	Buffalo grass	Moderate	70-80	Bda 98	Bgr 1	Few
North of Kearney	Buffalo grass	Overgrazed	50-70	Bda 90	Bgr 5	Many
Northeast of Kearney	Buffalo grass	Overgrazed	60-70	Bda 80	Bgr 15	Many

[1] Bda is *Buchloe dactyloides*; Bgr, *Bouteloua gracilis*; Scr, *Sporobolus cryptandrus*; Asm, *Agropyron smithii*; Bcu, *Bouteloua curtipendula*; and Afu, *Andropogon furcatus*.

erosion or deposit, trampling or drought, provided a suitable habitat for this species which thrives best in warm dry soils. It is not a good competitor and is easily replaced even by short grasses where they form a continuous sod. Tumblegrass is of quite similar distribution. It grows among the other grasses where the cover is thin and is sometimes the most abundant species locally in such habitats.

Plains muhly was not uncommon in ranges but was rarely found in great abundance. Penn sedge increased greatly during drought and, like involute-leaved sedge, occurred frequently and sometimes abundantly. Needle grass and needle-and-thread occurred only rarely and were never found in abundance. The bunch-forming hairy grama was found on dry banks and on other sites usually where the cover was open. June grass and Scribner's panic grass occurred somewhat sporadically and usually formed only a modicum of the vegetation. Species of three-awn grasses, nearly exterminated by the drought, were found only in certain parts of this great range area. They are almost worthless as forage. One was not impressed so much by the relatively small number of kinds of perennial grasses as by the extensive dominance of only a few.

WEEDY ANNUAL GRASSES

Certain weedy annual grasses were very abundant in many ranges and in spring they supplied much

forage. The three most widely distributed and of greatest abundance were little barley, six-weeks fescue, and hairy chess. Little barley germinates in fall or very early spring and becomes green and edible before much new foliage of the short grasses appears. This diminutive grass often grew thickly in the short-grass mats, especially in older and closely grazed ranges or portions of ranges (Fig. 41). It occurred regularly even where the basal cover was very high, 80-95 percent. In open ground or in dunged places the usual height of its slender unbranched stems often doubled or tripled and reached a level of 12-16 inches. In spring, little barley alone or intermixed with the short grasses provided fairly good forage. But normally early in June and for many weeks thereafter dense yellowish patches or continuous stands of dried plants in the short grass cover gave tone to the landscape, just as the early greening of pastures was due to this species. Little barley is a native of mixed prairie and a normal component of the short-grass cover. In badly depleted ranges during drought, this weedy annual alone sometimes produced a ton or more of forage per acre (Weaver & Albertson 1943). It was much less abundant some years after the drought and in many pastures it occurred, if at all, in insignificant amounts.

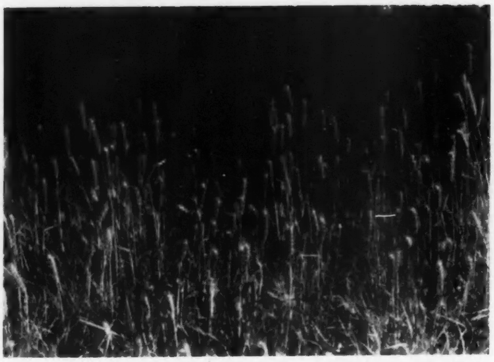

FIG. 41. Detail of little barley *(Hordeum pusillum)* growing in the sod of buffalo grass in the McCan experimental pasture near Kearney. Photo June 18, 1947.

The shorter and more spreading variety of six-weeks fescue *(Festuca octoflora hirtella)*, has habits of growth very similar to those of little barley. The densely aggregated stalks of this annual frequently clothed the bare places, whether small or large, that occurred between the tufts of short grass. On hillsides and ridges where it was sometimes still found abundantly it gave the range a tinge of brownish yellow even when the short grasses remained green. This grass decreased with increasing density of the short-grass cover, and in 1947 it was found abundantly only in poorer pastures. Its forage value was low.

Hairy chess was common in nearly all ranges except where it had been grazed out in spring. In depleted lowland areas it often formed a continuous cover or an overstory to other grasses in spring, and attained a height of 1.5 to 2 feet. It also occurred, sometimes abundantly, with western wheat grass and with open stands of mid and tall grasses as well. It was most conspicuous in short-grass ranges, since the plants, which dry and bleach to a light gray in midsummer, often remained standing until fall, quite above the short grasses. This species of brome, which came in and spread widely during drought, has a high forage value in spring and early summer and the new young plants are eaten in fall.

NATIVE FORBS

Prairie plants other than grasses constitute a long list of species. Practically all are perennials, the annuals and biennials together composing only a small percentage. Many forbs decrease or may entirely disappear under long continued grazing. But ordinarily they are sufficiently abundant to provide a valuable variety in the diet of livestock grazing native ranges, and they deserve careful consideration. Drought destroyed many of the forbs on the loess bluffs just as it affected them adversely elsewhere (Weaver & Albertson 1940a, 1944). Many species almost entirely disappeared, others were greatly reduced in numbers and vigor. But during the several good years that have occurred since the drought the forbs have made considerable recovery. A survey was made of the forbs in 27 widely distributed pastures, which varied in size from 80 to several hundred acres; species have been listed for a group of 17 pastures according to the number in which they occurred. In another group of 10 pastures they have been listed according to their abundance. The lists might have been enlarged considerably if species in local habitats as ravines, banks, and other places especially favored in their water relations had been included. Species listed are those distributed more or less throughout the cover. Annual native forbs and introduced weeds are not included (Table 7).

Of the 29 species listed in 1943 (column A) only one occurred in all of the 12 pastures, but 15 were found in at least half of them. Species of cacti were found in only 5 pastures and they were never abundant. In fact, no forbs occurred in unusual numbers. Drought had taken its toll and recovery was just getting under way.

One of the most abundant species, the cone flower *(Ratibida columnaris)*, almost disappeared during drought but had increased rapidly from seed, by which means it survived during the dry years. This was true also of western ragweed *(Ambrosia psilostachya)* except that its rhizomes aided in survival (Weaver & Albertson 1944). The list includes many of the 10 most drought resistant species of the central area of the mixed prairie which survived when practically all others had succumbed. The lead-plant, which has increased far beyond its normal numbers in mixed prairie, is so highly relished by livestock that it was found under grazing only as scattered relicts. In pastures generally, there are always fewer species and smaller numbers of native forbs (except-

TABLE 7. Species of prairie forbs found most frequently in pastures. Of 12 representative ranges, numbers in column A indicate in how many each species occurred in 1943. Column B is the number of pastures in another group of 5 in which these forbs occurred in 1947. Columns 1 to 10, respectively, are the ratings for 10 other widely distributed ranges. The abundance of each species in a pasture is indicated according to a ranking on a 5-point scale (1, very abundant; 2, abundant; 3, common; 4, infrequent; and 5, rare).

Native Forbs	A	B	1	2	3	4	5	6	7	8	9	10
Ratibida columnaris	12	4	3	3	2	3	4	4	4	4	3	4
Solidago mollis	11	4	3	2	2	2	3	..	3	3	5	4
Kuhnia glutinosa	10	4	3	3	4	4	..	4	4	4	4	4
Liatris punctata	10	5	2	3	4	3	3	3	4	4	2	2
Lygodesmia juncea	10	5	3	2	3	3	..	3	4	3	4	3
Solidago glaberrima	9	4	4	4	5	5	4	..	4	4	5	4
Ambrosia psilostachya	8	5	3	1	3	..	3	..	..	..	2	4
Sideranthus spinulosus	8	4	2	3	1	2	3	..	3	4	3	4
Amorpha canescens	7	3	..	5	5	4	4	..	..	3	..	4
Aster multiflorus	7	3	4	4	5	5	4	4	4	4	5	5
Lithospermum linearifolium	7	3	3	4	4	5	5	..	4	4	5	2
Malvastrum coccineum	7	4	3	3	1	1	2	..	1	1	3	1
Artemisia gnaphalodes	6	..	2	4	3	3	2	3	4	4	4	4
Cirsium undulatum	6	5	1	4	2	..	3	3	3	3	4	3
Cathartolinum rigidum	6	4	4	4	3	3	3	4	3	4	5	2
Allionia linearis	5	3	4	5	5	..	..	..	5	..	5	4
Gaura coccinea	5	5	3	3	3	4	4	4	4	..	2	3
Opuntia species	5	4	..	..	..	..	4	..	3	5	..	3
Petalostemum purpureum	5	2	4	4	4	3	3	..	4	5	4	4
Vernonia baldwinii	5	5	1	3	..	..	4	..	3	4	5	4
Antennaria campestris	4	1	..	..	5	..	5	..	5	5	..	5
Echinacea pallida	4	3	3	4	4	4	4	3	4	4	5	4
Psoralea tenuiflora	4	4	..	..	..	..	1	1	1	2	..	1
Psoralea argophylla	3	4	3	5	5	..	5	4	3	..	..	3
Meriolix serrulata	3	2	..	..	..	..	4	4	..	..	..	5
Aster oblongifolius	2	2	..	5	5	..	..	5	..	..	..	4
Callirhoe involucrata	2	3	4	5	..	..	..	..	..	..	5	2
Cathartolinum sulcatum	2	1	4	5	..	3	4	..	4	5	..	..
Rosa pratincola	2	1	5	..	5	3	4	3	4	5	..	4

ing a few that become weeds) than in prairie. Moreover, as a rule, great decrease in amount of forbs indicated prolonged and severe grazing.

Cactus was abundant in only a very few pastures in 1946-1947 and entirely absent from many. Like the cactus, several of the forbs listed have little or no forage value. These include *Cirsium undulatum*, which is spiny, *Lygodesmia juncea*, *Ambrosia psilostachya*, *Sideranthus spinulosus*, and *Vernonia baldwinii*. The last shows a decided tendency to increase in low ground. The only shrub of considerable range in pastures was buckbrush. It sometimes maintained itself in low thickets along ravines and recurred on hillsides where there was an adequate supply of water. However, it was not usually a serious weed.

Other perennial forbs found in several ranges included *Geoprumnon plattense*, *Astragalus lotiflorus*, *Asclepias pumila*, *Cirsium ochrocentrum*, *Solidago rigida*, *Pentstemon albidus*, and *Petalostemum candidum*. In fact, relicts of nearly all of the prairie forbs were seen in various ranges.

Native annual forbs of greatest local abundance were *Plantago purshii* and *Hedeoma hispida*. *Euphorbia marginata* Pursh was conspicuous where abundant on low ground in late summer and fall.

The chief introduced weeds were hoary vervain (*Verbena stricta*), prostrate vervain (*V. bracteosa*), and especially horseweed (Figs. 42 and 43). The first is an indicator of a broken cover and, if abundantly and widely distributed, it indicates pasture abuse. The low growing verbena properly belongs to the subsere and it is found only where a good plant cover has not been maintained. Horseweed varied greatly in amount from year to year. When weather in spring was favorable for its germination and establishment it occurred throughout most ranges in stands of variable density. Where the cover of grasses was good and competition for water great, the plants were usually dwarfed to 8-12 inches in height, but in more open cover a stature of 2 to 3 feet was often attained. When young, this weed was consumed with the grasses, and where grazing was frequently repeated there were few of them. But elsewhere, once they were half developed they were not eaten and grew in stands so thick as greatly to hinder later grazing. In good years they were so abundant and so widely distributed as to give the ranges a green tinge even during periods when the grasses were drying.

FIG. 42. Gumweed (*Grindelia squarrosa*) and hoary vervain in an old pasture. The vervain has a much more general distribution than the gumweed.

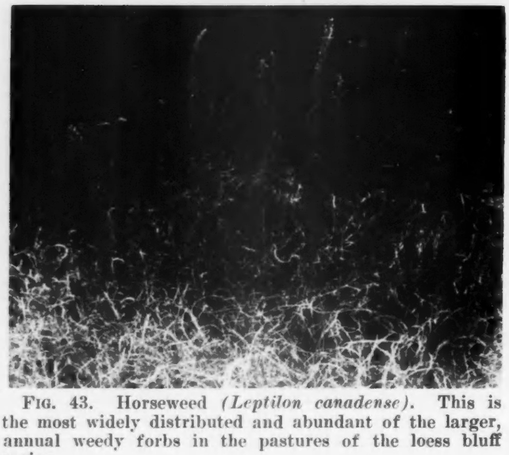

FIG. 43. Horseweed (*Leptilon canadense*). This is the most widely distributed and abundant of the larger, annual weedy forbs in the pastures of the loess bluff region.

SUBSERES

Some low-grade pastures have resulted from abandoning cultivated land. These were usually on such steep slopes that the land should never have been broken. For many years annual and perennial weeds constituted the bulk of the scanty cover of vegetation. Perennial grasses enter and increase slowly (Fig. 44). A single example must suffice.

FIG. 44. A steep hillside where the prairie had been broken about 25-30 years earlier. The succession has now reached the red three-awn-buffalo grass stage. The rounded bushes are the perennial brownweed *(Gutierrezia sarothrae)*. Many prairie forbs are present; sand dropseed *(Sporobolus cryptandrus)* and tumblegrass *(Schedonnardus paniculatus)* are common, but there is no blue grama.

A 23-year-old subsere was studied in the Sheen pasture (Fig. 45). Development toward the climax vegetation was far more advanced on the level land with Holdrege silt loam. Only 2 out of 20 of the 100-square-foot sampling plots had a foliage cover less than 50 percent and in most the cover was 70 to 85 percent. Sand dropseed was the most abundant grass in about two-thirds of the areas sampled, and supplied 58 percent of the cover. Buffalo grass ranked first in only one-fifth. Other important grasses were western wheat grass and hairy chess.

FIG. 45. View of western wheat grass (5 dark streaks in foreground) alternating with purple three-awn *(Aristida purpurea)* and buffalo grass (light colored). Portion of 23-year-old subsere in the Sheen experimental pasture. Photo June 18, 1947.

Little barley, three-awn grasses, and tumblegrass were common and widely distributed. Chief weedy forbs were hoary vervain, prostrate vervain, and a spurge *(Chamaesyce glyptosperma)*.

On the slopes on the Colby silt loam soil the vegetation was much thinner. Here the foliage cover ranged from 30 to 45 percent in 9 plots, 50 to 55 in 26, and 60 to 65 in only 13. Only 4 of the 52 plots had a good cover, 70-80 percent. Three-awn grasses (annual and perennial) provided two-thirds of the cover in a third of the plots. Sand dropseed was second in abundance and quite as widely distributed. Western wheat grass and buffalo grass were next in importance. Where the topsoil had washed away, native perennial plants had great difficulty in becoming established. The scarcity of legumes in the subsere was marked.

Some success has been attained by disking low grade pastures in early spring, thus leaving the established patches of buffalo grass, and seeding to blue grama with seed of buffalo grass and side-oats grama intermixed. But much success was obtained only in good years and failures were common, since the unfavorable conditions included the lack of a sufficient dead mulch, in addition to drought and erosion. When warm-season grasses as big bluestem, little bluestem, and side-oats grama were seeded in spring following a crop of smallgrain, Sudan grass, or sweet clover, better results were obtained. This was partly due to an increased supply of nitrogen and in part to a protective dead mulch. The very drought- and cold-resistant crested wheat grass may do well if seeded late in fall so as to escape damage from grasshoppers. Like Hungarian bromegrass, it should be drilled on the contour. Usually bromegrass does less well on the hills than crested wheat grass, but good stands are fairly certain in the valleys. Despite the great difficulties of reestablishing a permanent cover, the need for such a cover is so great that extraordinary efforts should be made to reclaim abandoned fields and to restore a complete cover on depleted ranges. The need is almost desperate; the price of neglect is the loss of the soil and the disturbance or destruction of the plant cover where the eroded soil is deposited. Erosion on these bluffs is so prevalent that almost every rancher and farmer is well aware of this danger.

EXPERIMENTAL PASTURES

Two pastures were selected for a study of the monthly and annual yield and consumption of forage in the several pasture types. In addition careful account was made of the manner and places of grazing during 1945-47, inclusive. The pastures were selected near Kearney because of their convenience for study, since the second author was in residence at that city. In the Sheen pasture consumption of forage alone was ascertained the first year, and both yield and consumption the second. Because of the great reduction in the size of the herd, study was not continued in 1947. But in the McCan pasture both yield and consumption of forage were ascertained during each of three years.

Methods

The methods were the same as those used by Weaver and Darland (1948) in their 4-year study of native pastures near Lincoln, Nebraska. Several sampling areas of about 10 square rods each were selected in each of the several grazing types. In each sampling area, one 30-square-foot exclosure, with its grazed control of similar size, was located in early spring. It was moved to a new location in this area at the end of each of the months of the grazing season.

In selecting the original location for an exclosure, two places were chosen within 10 to 15 feet of each other in which the vegetation was as nearly alike as possible. In one, the vegetation was to be clipped after a month of protection; the other, which was subjected to grazing, was also to be clipped at the same time. A coin was tossed to determine which of the two areas was to be protected. The exclosure was then set in place and stakes were driven into the soil in each corner to keep it from being pushed aside. Since the sides of the exclosure sloped inward from the base, it was not disturbed by the livestock. The control area was also clearly marked. At the end of each month at the time of the clipping, new places for the exclosure and control were selected in the same general area. These were as nearly as possible like the former control area and were selected before clipping, since both of the former plots were now to be clipped by hand close to the ground, closer than the cattle could graze. By subtracting the dry weight of vegetation of the control from that obtained from the exclosure, the monthly consumption from the 30-square-foot area was obtained (Fig. 46) (Fuelleman & Burlison 1939; Joint Committee 1943).

It was assumed that the average yield in any type during the first month was represented by the air-dry forage under that exclosure, since all debris from the previous year was carefully separated from the new vegetation and discarded. During the second month total yield was the amount that grew on the area newly exclosed less the amount of new vegetation remaining ungrazed in the control area of the preceding month. Clipping was uniform at all times, since one of the writers was in direct charge each month (Klingman, Miles, & Mott 1943). An example of the results in 1946 from an exclosure and control in buffalo grass in the McCan pasture is shown in Table 8. The average monthly consumption and yield as determined by the several exclosures are shown in graphs.

FIG. 46. View in the northern part of the McCan experimental pasture showing several of the movable exclosures used in determining consumption and yield. The area under each is 30 square feet.

TABLE 8. Amount of new forage harvested from an exclosure on a nearly level hilltop and from its control each month in 1946. The air-dry weights are in grams.

	May	June	July	August	Sept.	October
Exclosure	380.0	373.8	342.8	275.3	259.7	233.7
Control	307.5	246.3	193.3	231.3	231.7	202.0
Amt. consumed	72.5	127.5	149.5	44.0	28.0	31.7
Exclosure	380.0	373.8	342.8	275.3	259.7	233.7
Control of preceding month	0.0	307.5	246.3	193.3	231.3	231.7
Amt. of yield	380.0	66.3	96.5	82.0	28.4	2.0

Sheen Pasture

This pasture was on typical loess bluffs 4.5 miles west of the city of Kearney and ½ mile north of the Kearney canal, which here is at the foot of the bluff region on the edge of the Platte River Valley. The hills are about 120 feet higher than the lowest ravines (Fig. 47). The general elevation is about 2,300 feet. The pasture consists of 160 acres of rolling, much dissected land, characteristic of the region. The slope varies in steepness from 8 to 21 percent, but some slopes below the high banks of ravines, still clothed with vegetation, are as steep as 68 percent. The soil is Colby silt loam, except about 25 acres of nearly level land on the west end of the pasture which is Holdrege silt loam. About 80 acres of the west part of the pasture was broken in 1925. The pasture is surrounded on all sides except the south by extensive areas of range land.

Grazing Types

Vegetation in the pasture was not uniform but consisted of four communities or types. The buffalo grass type occurred on land with rolling topog-

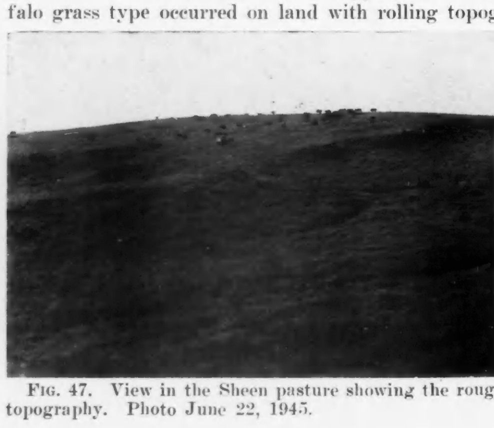

FIG. 47. View in the Sheen pasture showing the rough topography. Photo June 22, 1945.

raphy. This included rounded hilltops and gentle to steep slopes which ended abruptly on their lower sides at the steep banks bordering the eroded valleys (Fig. 48). Here a fringe of side-oats grama, western wheat grass, and other taller grasses was found.

FIG. 48. Typical view on a long slope of about 10 percent in the buffalo grass type. Irregularities in the cover are due to clumps of little barley especially well developed in spots that have been fertilized. Photo June 22, 1947.

This pasture type was one of the most extensive and supplied by far the largest part of the season's forage. There was very little blue grama anywhere, seldom over 5 percent, but little barley grew thickly even in the dense short-grass sod. Small amounts of western wheat grass were common. The average basal cover was about 85 percent.

The sand dropseed-buffalo grass type covered most of the flat upland where grazing throughout many years had been most severe. Consequently it was most damaged by the prolonged drought (Weaver & Albertson 1940). It was undoubtedly at one time in the buffalo grass stage of degeneration of mixed prairie. Because of less runoff, this was probably a more productive type than the present one dominated by sand dropseed. In this community the sand dropseed formed a more or less continuous cover (Fig. 49). But in it were relict, often circular patches of buffalo grass. These had increased regularly but slowly in size since the close of the great drought and with newly established patches now occupied a fourth to a third of the soil surface. But the sod was more open than that on the hillsides. The discontinuous patches varied from a few feet to several yards in diameter, and the increase in size was at the expense of sand dropseed. There was, in general, much more open ground here than in the preceding type. Hence such forbs as western ragweed, hoary vervain, red false mallow *(Malvastrum coccineum)*, and others occurred in greater abundance as did also several species that were not found regularly in the closed cover. Here little barley was better developed than in the buffalo grass sod and tumblegrass was more plentiful.

On the level 25 acres of the part of the pasture

FIG. 49. General view in the sand dropseed-buffalo grass type. The light colored places are small patches of buffalo grass. In the darker places the rather open cover is mostly sand dropseed.

once broken, the sand dropseed-buffalo grass type had developed as a distinct successional stage. Except that it was much weedier than this type on the unbroken land, the two were almost identical. Basal cover throughout the sand dropseed-buffalo grass type averaged about 70 percent. With few exceptions blue grama occurred only in small amounts and most abundantly in rough places where it had survived the drought.

A third community, the buffalo grass-bluegrass type of lowlands, received runoff water in addition to the precipitation. Moreover, snow is blown from the hills into the valleys or is lodged on the slopes and in melting adds moisture to these lowlands. This additional soil moisture was reflected not only by the presence of Kentucky bluegrass, many coarse sedges, and various species of mesic grasses, but also by the rank growth of the vegetation in early spring. The presence of buckbrush and certain other shrubs, often in considerable abundance, was further evidence of the more favorable supply of soil moisture (Fig. 50).

Although the most abundant species was buffalo grass, bluegrass was also found abundantly. Locally it occurred in nearly pure stands in the most mesic sites, but it was often intermixed with buffalo grass on these lowlands. It was the most abundant grass and often the only one growing in the thickets of buckbrush. Eventually this species was sought out, even here, and closely grazed. On the valley floor there also occurred relict plants of big bluestem, penn sedge, and Scribner's and Wilcox's panic grasses. Here also side-oats grama was found but more plentifully, as was also big bluestem, on the slopes. Only a trace of little bluestem remained but numerous prairie forbs occurred as relicts on the rough banks. Western wheat grass, as in the other types, occurred in small widely scattered patches. It was here that hairy chess reached its greatest density

FIG. 50. Cattle grazing in the buffalo grass-bluegrass type in one of the several valleys in this pasture. This is a side canyon near the windmill and it has been grazed closely. Note the buckbrush in the valley and on the steep bank in the foreground.

of stand and greatest stature. In early spring it overtopped all the other grasses and provided much palatable forage during a period of about six weeks. Ordinarily it is not all eaten, but remains in patches or as an open network of dried, unpalatable forage which greatly hinders uniform grazing thereafter. An average basal cover of 82 percent was ascertained in this type.

The three-awn grass type covered all of the slopes on the west 80 acres except a small percentage consisting of steep banks that were left unplowed. Chief perennial grass was purple three-awn. Its bunches, however, were so widely spaced that they alone did not form a complete cover. Intermixed with them in large amounts was the annual, prairie three-awn (*Aristida oligantha*). This short-lived grass produced so much of the foliage cover that alive or dead it played a remarkable role in protecting the soil from erosion. Neither of these subsere grasses was grazed in any amount, if at all. Of valuable range grasses, the order of abundance was sand dropseed, buffalo grass, western wheat grass, and small amounts of side-oats grama. Sand dropseed was rather generally distributed throughout. Buffalo grass occurred only in widely spaced, small patches and did much toward stabilizing the soil which erosion had reduced to such low fertility that the grass was only half as tall here as on the level land that had maintained its topsoil. Western wheat grass occurred in streaks and patches and was widely distributed in locally open stands (Figs. 51 and 52). It was often dwarfed. The soil beneath it was usually bare. In addition there were small amounts of blue grama as isolated clumps and also tumblegrass. There was much erosion of the light colored, flour-like loess around the bunches. Many of the bunches of blue grama were elevated 5 to 6 inches above the present soil surface.

Although some prairie forbs and especially *Astragalus shortianus* and *Malvastrum coccineum* were common to abundant, in some places on the thinnest soil there were few perennials. Here there was a thin cover of hairy chess and little barley. Frequently weeds were abundant; wavy-leaved thistle occurred in large patches, open stands of hoary vervain were everywhere, and horseweed was plentiful. Even the annual sunflower (*Helianthus annuus*) was common. On steep slopes to nearly level land the soil surface was uneven and rough from erosion; on some slopes the soil was almost bare (Fig. 7). Often soil erosion was more rapid than soil formation. An average basal cover of only 40 to 60 percent was found in the three-awn grass type.

FIG. 51. View in three-awn grass type on a steep hillside. The encircled patches are buffalo grass, the dark one in the foreground and another in the distance are western wheat grass, but the most extensive vegetation is three-awn grass. Bunches of purple three-awn show plainly at the left beyond the western wheat grass.

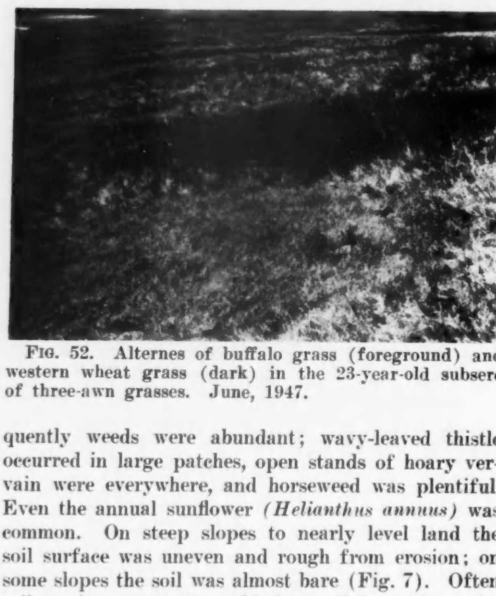

FIG. 52. Alternes of buffalo grass (foreground) and western wheat grass (dark) in the 23-year-old subsere of three-awn grasses. June, 1947.

Of approximately 70 species of forbs found in this pasture, only about 15 were common to abundant. These were among those previously listed.

GRAZING IN 1945

During a period of six weeks after May 5, when 55 head of cattle (55 animal units) were placed in the pasture, grazing was heavy in the lowland buffalo grass-bluegrass type. For not only was bluegrass the earliest perennial in beginning growth but also it was here that the winter annual, hairy chess, made its best growth and was most abundant. The

cool, moist weather of spring and early summer promoted an excellent development of the cool-season bluegrass and winter annuals. Moreover, this type had been grazed closely the preceding year and there was no dried forage to hinder grazing. The unconsumed hairy chess of 1944 had been trampled to the ground during the fall. Although the herd ranged widely over the uplands in search of the new crop of little barley and hairy chess, green foliage there was relatively less abundant. There were more of these weedy annual grasses in the more open cover of sand dropseed than where buffalo grass formed closed stands. Small amounts of green forage were also obtained from western wheat grass. During late May and in June the new crop of buffalo grass became available for use. This heavy early grazing in lowland and smaller amounts in the other types is shown by the graphs of consumption in Figure 53.

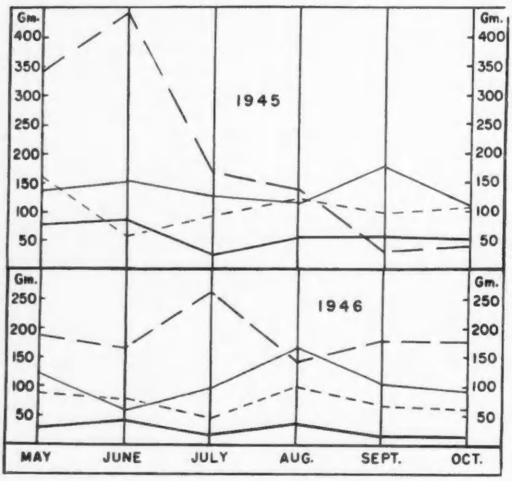

FIG. 53. Average amount of forage in grams consumed per unit area (30 square feet) in the buffalo grass-bluegrass type (heavy, long broken lines), the buffalo grass type (light continuous line), the sand dropseed-buffalo grass type (light, short broken lines), and in the three-awn grass subsere (heavy continuous line) in 1945 and 1946.

With the ripening of hairy chess, which overtopped all of the lowland grasses and equaled the height of western wheat grass, grazing in the lowlands became much less pronounced.

In late June and July the highly palatable sand dropseed made an excellent growth. Forage in this type was usually well developed before it was much grazed. It was consumed, along with the accompanying buffalo grass in considerable amounts in July and August and this type supplied good grazing in the fall. Except for a single period of drought in July, the vegetation grew well throughout the summer. With the decline of grazing in lowlands, consumption of buffalo grass on the uplands, where it made an excellent growth in July and until mid-August, became greater and reached a maximum during September (Fig. 53). Grazing late in fall resulted in the removal of practically all of the forage in areas of buffalo grass that had previously received little attention from the cattle. These were on the steeper slopes.

In late fall search for green forage was general, grazing was close, and there was much trampling. The dry hairy chess and various weeds, especially in the valleys, were trampled to the ground. Bluegrass beneath the buckbrush, heretofore unmolested, was now grazed closely and the buckbrush was much trampled. Consumption of forage in the three-awn grass type was uniformly low throughout the summer.

By November 5, very little edible residue was left anywhere on this range, which was greatly overgrazed despite the fact that the cattle also had access to a field of 80 acres where there was a poor stand of sweet clover. No exclosures were maintained in the buckbrush or other roughs, hence the extent of this late grazing is not shown in the graphs.

GRAZING IN 1946

Grazing began on April 28 when 32 cows and 8 six-months-old calves (about 36 animal units) were turned into the pasture. The spring was early but dry (Fig. 54). On the uplands little barley and buffalo grass were 1.5 to 3 inches tall but new stems were too scattered to provide much forage. Hence, most of the early grazing occurred in the buffalo grass-bluegrass type. Even there the dominant grasses were only an inch or two high; but a little western wheat grass and considerable amounts of hairy chess formed an overstory at 2 to 4 inches almost throughout.

Moderate drought continued throughout May. On the dry slopes buffalo grass had made very poor growth. On the more level lands, where sand dropseed was also a dominant, the 2-inch buffalo grass was slightly exceeded in height by sand dropseed. Little barley, scattered thickly throughout, was heading at 1 to 4 inches. The scattered patches of western wheat grass had new shoots 4 to 8 inches tall, and hairy chess, averaging somewhat taller, was more widespread. Grasses in the subsere were likewise poorly developed. In fact, scarcely any new forage occurred on eroded slopes. Consequently, grazing on the upland was light, and much of the forage was obtained from the lowland (Fig. 53). Here a fairly continuous stand of buffalo grass 3 inches high, intermixed with bluegrass in the more moist places, was obscured by a 6- to 8-inch stand of hairy chess or, in places, by little barley.

Drought continued until late in June (Fig. 54). Both level upland and hillsides became dry. Grazing was very light on uplands and even more confined to the valleys where the grasses were still green and growing (Fig. 53). But late in June forage in the lowlands was largely exhausted, since the winter annuals had almost ceased growth. Bunches of side-oats grama and big bluestem, as well as bluegrass, although well protected by buckbrush or ironweed *(Vernonia baldwinii)* had been sought and closely

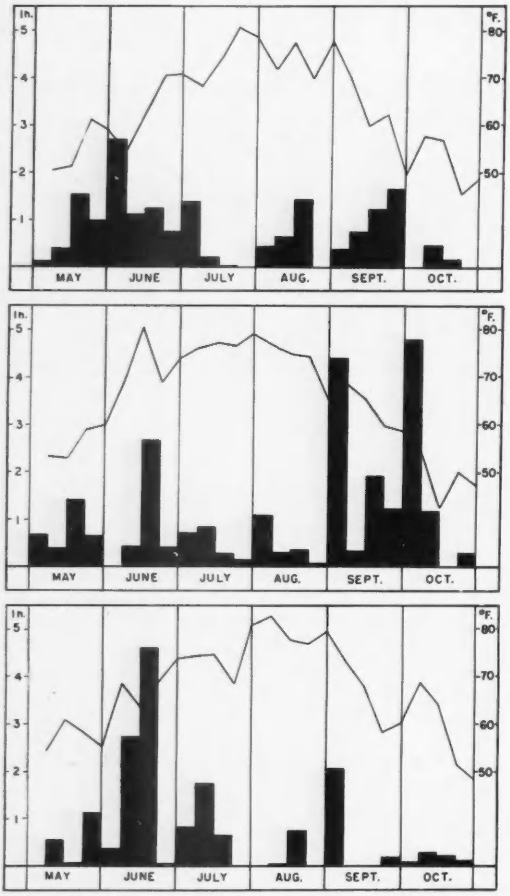

FIG. 54. Total rainfall at Kearney, Nebr., in inches (approximately) by weeks, and average weekly temperatures in degrees Fahrenheit, during the seasons of 1945 (upper), 1946, and 1947 (lower), respectively. In 1945 and 1947 the first week charted is May 5 to 11, in 1946, May 2 to 8.

grazed. Although the valleys were kept closely grazed, grazing in the buffalo grass type became more pronounced and was encouraged by a good growth of forage following heavy rains.

Rainfall in late June and in July was sufficient to moisten the entire surface foot of the soil. Buffalo grass developed rapidly and supplied much forage. Preference of the livestock for sand dropseed encouraged much grazing in the sand dropseed-buffalo grass type, but the foliage was more sparse than in pure buffalo grass. Both three-awn grasses had developed well and dominated the subsere; cattle appeared to avoid the entire area. Both bluegrass and buffalo grass were repeatedly grazed to an inch or less in the valleys, except where they were protected by maturing western wheat grass or hairy chess. Various species of Carex and Cyperus were sought and grazed closely.

Buffalo grass made fair to good growth during August. Despite the fact that dried stems were usually intermingled with green ones because of mild drought, grazing was regular in this type, since all of the forage was of the current year's growth. Sand dropseed was eaten in preference to buffalo grass throughout the entire summer, but its foliage was sparse and the flower stalks were scattered. Hence, the sand dropseed-buffalo grass type supplied less forage per unit area. In the subsere both the three-awn grasses had increased greatly in density of stand. The plants were 4 to 12 inches high and seed was abundant. The scattered bunches of sand dropseed, patches of western wheat grass, and even buffalo grass remained almost ungrazed in this type even in late fall. The buffalo grass-bluegrass type continued to provide considerable forage, although much less than during July (Fig. 53).

Growth of buffalo grass decreased in September and there was little or no green foliage. Lower temperatures and abundant soil moisture had promoted thick stands of both hairy chess and little barley, but the plants were small and supplied only very little forage even in October. Forage on some areas was practically all consumed. Renewed growth of bluegrass, sedges, and various perennial grasses in the valleys resulted in increased forage consumption (Fig. 53). During October grazing decreased slightly on the uplands, but continued heavy grazing occurred in the valleys. The remaining protected areas were grazed and nearly all forage of the current year was consumed.

COMPARISON OF CONSUMPTION AND YIELD

Portable exclosures were placed in 8 sampling areas the first year but the number was increased to 18 the second. This permitted quantitative study in 4 or 5 sampling areas in each of the four types. Since the grass under each exclosure and its control was clipped each month, this involved the clipping of 216 30-square-foot areas in 1946. A comparison of graphs of consumption during the 2 years, shows clearly that it was usually lower in 1946 (Fig. 53). This was due in part to the reduction in number of animal units from 55 in 1945 to 36. Consumption in the buffalo grass type was consistently lower except in August. Seasonal consumption was 1.03 tons the second year compared with 1.30 tons the first. Except for June, 1946, less forage was consumed each month in the sand dropseed-buffalo grass type also. Seasonal consumption was 1.03 and 0.71 tons during the two seasons, respectively. The decrease in consumption on the uplands in fall was due in part to preference for the green forage in the valleys, which was kept green in 1946 by much rain in autumn. In the seral type consumption was greatly reduced each month of the second summer and total consumption was 0.24 ton per acre compared with 0.57 the preceding year.

Compared with 1945, the lowlands were grazed proportionately more than the upland in 1946. This resulted partly from the drier year and partly be-

cause of a decrease in the total demand for forage. Much less forage was produced on the lowland in 1946 because of the drier spring and consumption was correspondingly lower compared with 1945. But thereafter grazing was consistently so much greater here that seasonal consumption of the smaller herd (1.78 tons per acre) was almost as great as that of the larger one (1.86 tons) of the preceding year.

The relation of consumption to yield in the several types in 1946 is shown in Figure 55. Where yields were highest on the upland (in the buffalo grass type), they were three times greater than consumption in May and about twice as great in June. By the end of July consumption equaled the yield, after which the cattle lived partly and later largely on forage previously produced. High production in the sand dropseed-buffalo grass type was likewise great in May. Here also, it was due largely to the winter-annual grasses. On this dry upland, annual grasses grew poorly in June and the early yield of sand dropseed was low. But forage was produced rapidly in July following abundant rainfall. As in the preceding type, yield was consistently lower than consumption in late summer and fall. Because of the abundance of the unpalatable three-awn grasses, yield in the seral area was usually two to three times greater than the amounts of palatable grasses consumed.

The more moist lowlands, characterized by the buffalo grass-bluegrass type but including various tall and mid grasses and a heavy cover of winter annuals, produced the highest yields throughout of any type. The high yield in July is a direct reflection of good rainfall and runoff water from the slopes. Although the excess of yield over consumption was not great, it was maintained until September. Of the excellent yield (2.19 tons per acre) 1.78 tons were consumed. Only 19 percent, consisting largely of coarse stubble and uneaten residues of winter annuals, remained on the soil.

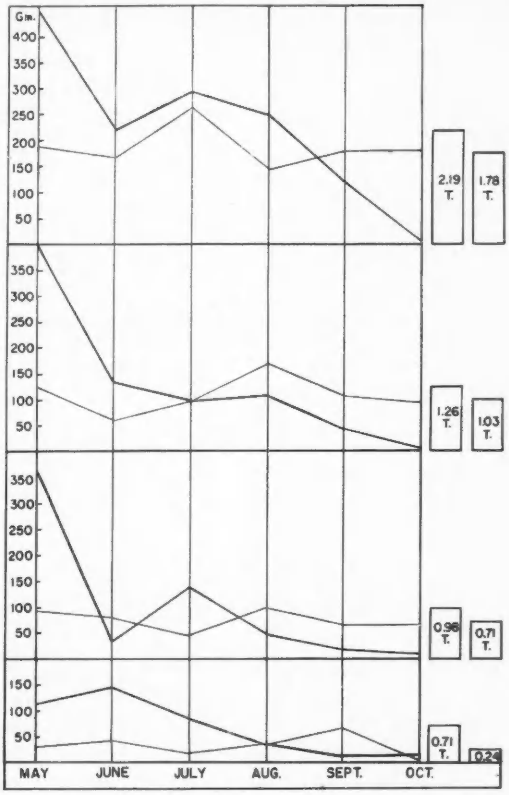

FIG. 55. Average yield (heavy lines) and average consumption (light lines) in grams per unit area in each of the four grazing types in the Sheen pasture in 1946. Seasonal yields and consumption are shown in tons per acre. From top to bottom the types are buffalo grass-bluegrass, buffalo grass, sand dropseed-buffalo grass, and three-awn grass.

McCan Pasture

This pasture of 70 acres is one mile northwest of Kearney. It includes three large, round-topped or partially flat-topped hills. They extend in a general east-west direction with narrow intervening valleys. The hills are 40 to 50 feet above the valleys, and the slopes are only moderately steep. The slopes often give way abruptly to steep banks which border the ravines. The valleys, with a single exception, have no ditches but are well-sodded rounded depressions (Figs. 56 and 57). An abundant water supply is available at the south end of this half-mile-long pasture, a well being located in the 10 acres which is used for buildings and farmyard. There is a large pasture on the east; the west side is protected by a road from blowing dust; there is also a road on the north side, otherwise this pasture is surrounded by cultivated fields. The soil is Holdrege silt loam and it is fairly deep. In the mature soil of level upland the lime layer occurs at a depth of 36 inches.

By the latter part (1939-1940) of the seven years of drought the pasture had lost nearly all of its cover of perennial short grasses. This was an almost general phenomenon in the mixed prairie (Weaver & Albertson 1940). It was in the first weed stage (Weaver & Albertson 1944). Only sparse patches of short grasses remained. These were mostly buffalo grass but small amounts of blue grama also occurred. The owner feared that the pasture was ruined. He harrowed the land in order to loosen the Russian thistles *(Salsola pestifer)* so that they might be blown away. This flattened sunflowers, lamb's quarters, and pigweeds on the ground, which was advantageous to buffalo grass in relation to light. This grass developed rapidly with the cessation of drought. Thus, from a wilderness of weeds the succession proceeded so rapidly that in 1945 revegetation was nearing completion. This was due largely to the excellent growth and rapid spreading of buffalo grass, which has been described by Weaver and Albertson (1944) as a general phenomenon of the central mixed prairies.

FIG. 56. General view in the southern part of the McCan pasture showing nature of the topography and the excellent cover of buffalo grass in which there are relatively few weeds. Positions of several exclosures in 1947 are indicated by x.

FIG. 57. Cattle grazing on the lowland of the McCan pasture on June 19, 1947. Grazing on the uplands was not general.

By 1943 buffalo grass carpeted the valleys and sides of even the steepest slopes. Blue grama resisted extinction by drought on the drier hilltops where buffalo grass succumbed, and had healed over all but a few of the formerly extensive bared places. The last remnants of such subsere weeds as annual sunflower, lamb's quarters, and horseweed were represented by old stems only in 1945. While the basal cover varied from 60 to 95 percent, the average percentage was about 80. Little barley was an important component of the grassland. It formed a continuous and often thick cover except on the most grazed ridges. Often there were 200 to 250 plants per square foot. In spring it gave a yellow-green tone to the landscape, since it was practically continuous over three-fourths of the pasture despite the dense sod.

The most abundant and most widely distributed grass, except on certain ridges where blue grama grew locally in nearly pure stands, was buffalo grass. Other species, in order of their importance, were Kentucky bluegrass, found only in the valleys, western wheat grass which occurred sparingly on both slopes and in valleys but constituted 5 percent or less of the cover, and big bluestem in the valleys or as remnants with side-oats grama along the banks of the lower slopes. Six-weeks fescue was scattered widely but in small amounts. Sand dropseed was widely but sparsely distributed as a relict from the early grass stage. Hairy chess and downy brome were almost rare as were also tumblegrass and hairy grama. All of these grasses, with the single exception of western wheat grass, were kept closely grazed.

Among approximately 70 native forbs only about 10 were common to abundant. These were *Grindelia squarrosa, Hosackia americana, Psoralea argophylla, Ambrosia psilostachya, Gaura coccinea, Liatris punctata, Ratibida columnaris, Malvastrum coccineum, Ionoxalis violacea* and *Cathartolinum rigidum*. Grindelia and Ambrosia were rarely eaten and the others provided only a small amount of forage. A considerable number, as *Astragalus shortianus, Geoprumnon plattense, Oxytropis lamberti, Parosela enneandra*, and *Sideranthus spinulosus*, were of local occurrence and grew mostly on the steep banks. Repeated grazing and the dense sod of buffalo grass, which covered the soil like a thick rug, suppressed the forbs.

Except for *Grindelia squarrosa, Ambrosia psilostachya*, and *Leptilon canadense* (in certain years) the pasture was remarkably free of weeds. Grindelia was sufficiently abundant only on a few slopes to interfere with grazing, and patches of Ambrosia were small. Others of much less importance were *Verbena stricta* and *Cirsium undulatum*. The soil had a continuous cover of litter a few millimeters thick, and bare ground was seldom exposed.

GRAZING IN 1945

From early spring until mid-June grazing by 13 cattle and 5 horses (18 animal units) was mostly confined to the valleys. The spring was cool and moist and little barley grew in great abundance and was highly preferred to buffalo grass. After grazing to a height of 1 to 2 inches, this weedy, winter annual recovered rapidly and was repeatedly grazed. Amounts removed were 463 grams per exclosure or ¾ ton per acre in May, and 255 grams in June. Little barley was scattered thickly over the uplands as well. In grazing here some buffalo grass was also consumed. Since little barley was 4 to 6 inches tall and the new buffalo grass only 2 inches as late as June 5, it seems certain that the bulk of the forage was little barley (Fig. 41). Forage of the previous year's growth need not be considered since it was flattened on the soil by heavy rains and wet snows of early spring, and lay below the grazing level.

After the little barley had produced its spikes (and in the previously grazed patches had ceased growth and began to dry) there was a transition in the grazing trend away from this grass and toward the rapidly developing buffalo grass. This transition period occurred late in June. Thus, from early July to the middle of August grazing was almost exclu-

sively in places which had been closely grazed the preceding year. Here the young buffalo grass was very much liked, and it was consumed in considerable amounts. In general these places were on the hilltops and upper slopes and in the valleys, but they also occurred on lower slopes. During this period the mid-slopes or other places where previous grazing had been light (approximately half of the pasture) were scarcely grazed.

By the middle of August a third shift in grazing occurred. Available soil moisture was almost exhausted and temperatures were high (Fig. 54). Grasses in the most favored grazing areas were dry and had ceased growing. Hence, thereafter grazing was done on the mid-slopes where the vegetation was dense but still green. It was less palatable, partly because of the intermixture of the dried stems of little barley. Because of light rains in August the grass remained green for several weeks. The buffalo grass dried permanently about September 1, but it was grazed long after it was cured (Fig. 58). Small amounts of bluegrass, various sedges, and big bluestem were also closely grazed where they grew in the valleys. Dense stands of little barley were promoted by the fall rains but the plants failed to reach a height sufficient to supply much late grazing. On the hillsides old grazing areas were enlarged, new ones were started, and the cured buffalo grass was removed in large amounts. Cattle were taken from the pasture early in November.

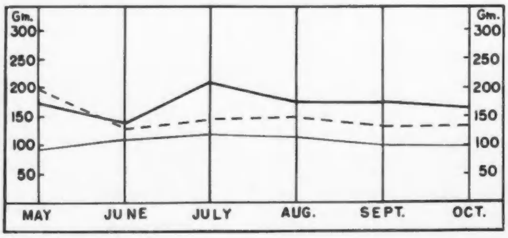

FIG. 58. Average amount of forage in grams consumed per unit area (30 square feet) in the McCan pasture each month of the growing season of 1945 (heavy line), 1946 (light broken line), and 1947 (light line). The amounts recorded for the month of May also include forage consumed earlier in spring.

At the end of the season it was clear that the southern half of the pasture near the well had been grazed about twice as heavily as the more distant northern half. On this more closely grazed part about two-thirds of the vegetation was uniformly removed to 0.5-1 inch and much of the remainder to 2 inches. Perhaps one-fourth of the area, especially on the steeper slopes, was lightly grazed to 4 inches. In contrast, in the more distant half about one-third was closely grazed but the rest was little grazed except in patches of a few square feet. Over most of this lightly grazed part new foliage was 5 to 6 inches tall but some had been removed to a height of 3 to 4 inches. There was a distinct preference for grazing in more open stands of buffalo grass rather than in places where the foliage was very heavy and densely matted.

GRAZING IN 1946

Livestock was turned into the pasture on March 25. There were 13 cattle and 5 horses as in the preceding year, but three steers were only yearlings. Hence the animal units were only about 17. Grazing during April was a continuation of the process started in autumn of reducing the amount of forage which had accumulated in 1945. Although little barley was thickly intermixed with buffalo grass throughout the pasture, its height growth did not exceed that of the short grass. It supplied some inducement for the consumption of the cured forage but added little to its bulk.

Little barley, because of dry soil and stunted growth in May, fell far short of providing an amount of forage equal to that of the preceding year. Nor was much green forage supplied by it in the valleys, despite the fact that here it was kept continuously grazed to 1 inch. Also the considerable areas formerly held by bluegrass were now almost all occupied by buffalo grass, which becomes green much later (Fig. 59). Hence, the cattle roamed widely over the upland as well, seeking the new green foliage of little barley. It grew tallest in places ungrazed the previous year, since here snow had accumulated and the dried forage protected the soil from high evaporation. Thus, all through the month large amounts of the last year's forage were consumed.

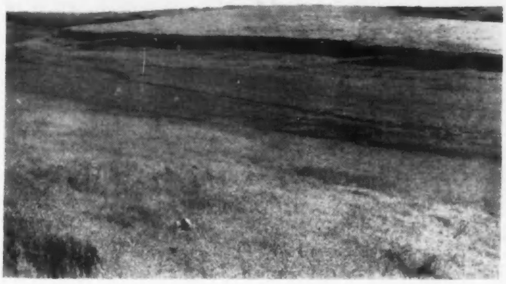

FIG. 59. Buffalo grass in a ravine. It has almost entirely replaced bluegrass. This sod, which was very dense in 1947, was maintained even a short distance from the windmill.

A similar type of grazing continued throughout June. Because of the drought the usually productive valleys provided comparatively little forage (Fig. 54). Moreover, the areas which had been closely grazed the preceding year, and more or less this year after the new growth gradually developed in May, were now dry and no longer grazed. This included fully half of the pasture. Hence, there was much selective grazing in areas previously ungrazed. This was not close and uniform; only the top 2 to 3 inches

was taken. Finally the entire area with taller foliage was grazed and most of it was reduced to a height of 3 to 4 inches.

Adequate rains occurred after the middle of June. Soon new forage developed in previously grazed upland areas and especially in the valleys so that grazing of the old forage was abandoned. There was a distinct shift to the type of grazing normal for this season, which was grazing in areas previously closely grazed.

Rainfall in July was sufficient to promote a fair to good growth of the grasses, although only the surface foot of soil was moist. In the valleys grazing was usually to a height of an inch. Grazing was also general on the slopes and hilltops and usually to 1-2 inches. Exceptions to close grazing occurred occasionally, especially at the north end, where some forage was reduced to a height of only 3 to 4 inches. Buffalo grass, owing to scarcity of available water, was much less luxuriant than in 1945. When periods of drought occurred, most of the buffalo grass became dry and dormant and hence less palatable on the general area where grazing had been close. But it remained green where protected by dry forage of the preceding year. Hence at these times there was a distinct shifting of grazing to these areas. This was especially pronounced late in August.

Rainfall during September was high and wet the soil to a depth of 2 feet. But temperatures were relatively low and the grasses grew very slowly (Fig. 54). Since there was scarcely any new forage produced the livestock gradually depleted that which remained. In October the soil moisture was replenished to a depth of 4 feet, but this scarcely affected the current year's forage production. Conversely, there was some leaching of nutrients and the value of the forage was reduced. The third of the pasture nearest the well was uniformly and closely grazed to 1 or even 0.5 inch. Similar conditions, except for a few small patches which were grazed high, maintained over the central part of the pasture. Even in the northern portion the extensive areas formerly grazed but little had been gradually reduced to a height of 2 inches, and even where the most debris remained in 1945 the grasses were grazed to a height of 3 to 4 inches. Formerly closely grazed places were kept in that condition. Thus, the entire pasture was grazed closely, or only a small portion moderately. In October, it seemed clear that practically all of the forage produced during the year had been consumed.

GRAZING IN 1947

Grazing began on April 28. The herd consisted of 12 animal units, 3 of which were horses. Since the grass had nearly all been eaten the preceding year and little new growth had occurred, there was scarcely enough forage to satisfy the animals. They ranged widely seeking out the dunged areas where the buffalo grass and little barley were somewhat taller. Although the sub-soil was moist to a depth of about 4 feet, vegetation developed slowly because of dry surface soil and continued unseasonably cold weather. Buffalo grass had not renewed growth and little barley was only about an inch high. Vegetation in the valleys, usually lush at this season, was even less developed than that on the slopes. The small amount of bluegrass that remained was stunted by drought. Milch cows received a grain supplement until the pasture improved (Fig. 58).

By May 15 the pasture was green everywhere. Although buffalo grass developed slowly, little barley grew thickly throughout and was 4 to 6 inches tall as were also many forbs. Forage in the valleys was growing rapidly and here the grass was kept closely grazed. This forage was preferred to any on the upland except that in the small, bright green, fertilized spots which were also kept closely grazed. During June general grazing continued in the lowlands but only selective grazing elsewhere. There was an abundance of forage in the valleys. The small remaining areas of bluegrass were kept closely grazed. On the upland the spikes of the thick, continuous stand of little barley were ripening at heights of 4 to 7 inches, and quite above the 2- to 4-inch buffalo grass, which grew rapidly only late in June, following heavy rainfall (Fig. 54). The livestock appeared well fed and spent much time at rest, which was quite in contrast to their continuous search for forage earlier in the season.

In July the spikes of little barley shattered. There was a luxuriant growth of buffalo grass usually 4 to 5 inches tall; forbs too were well developed despite their retarded growth in spring. The grazing pattern changed only slightly from that of June. The livestock had been unable to keep the lowlands uniformly grazed and they now spent some time on the slopes, especially the lower ones. The green, fertilized spots throughout the pasture were kept grazed to 1-1.5 inches, and there was a little light general grazing. Total consumption of forage was highest during July (Fig. 58).

By August 1 all of the little barley was dead and the heads were shattered. Six-weeks fescue was also disintegrating. The livestock found the luxuriant buffalo grass on uplands quite as attractive as vegetation in the valleys, where only recently grazed patches were utilized and the more rank growth was avoided. The livestock spent comparatively little time in grazing, so abundant was the forage, and seldom reached the more distant side of the pasture, where only the fertilized spots were kept grazed. Despite the fact that lower slopes near the paths were the most favored grazing places, only half of the grass on the lowlands was closely grazed.

Growth of vegetation decreased late in August, which was hot and dry, and later almost ceased. The livestock was no longer able to graze new forage in previously grazed places but was forced to feed on the mature forage in the ungrazed areas. This change in the grazing pattern was similar to that of the previous year and occurred at about the same time.

During September and October grazing consisted

almost entirely of consuming the forage which had been produced in summer. Subsoil moisture and a heavy rain in September kept the short grass in fairly good condition. It was green at the base. It was less succulent than when growing but palatable and nutritious.

The third of the pasture nearest the well was grazed to 1-3 inches. The central third was grazed only moderately; extensive areas occurred where the grass was 3 to 4 inches tall. Forage in the northern part of the pasture was abundant. Much of it was ungrazed and a height of 4 to 5 inches was common. In only relatively few places was the grass reduced to a height of an inch.

Summarizing, during the good year for growth, 1945, the pasture at the north end was somewhat undergrazed. In the dry year which followed, practically all of the forage produced was consumed. But with a reduction of the herd in 1947 from 18 to 12 animal units, and a good growing season (except for July drought) the pasture as a whole was undergrazed. With greatly varying seasons and minor cycles of wet and dry years, the proper adjustment of the size of the herd to a given range is indeed a difficult problem.

COMPARISON OF CONSUMPTION AND YIELD

In 1945 portable exclosures were used in 8 sampling areas in various sites in the 70-acre pasture. The number was increased to 18 in 1947. Monthly consumption during the three grazing seasons is shown in Figure 58. The graph for 1946 is remarkably similar to that of the preceding year. Both are quite regular throughout the grazing season. The fact that the horses and nearly all of the cattle were mature animals may account for this regularity. With growing stock there is usually a distinct upturn in quantity of forage consumption in September. With buffalo grass, however, there is little decrease in its nutritive value upon curing, a fact which may account for the uniform trend of the graph. Differences in amounts of forage consumed during the two years may be due to several factors. First is the decrease in the number of animal units from 18 to 17. Secondly, forage in general was less succulent during the drier year of 1946. Moreover, the amount available was much less than in 1945.

With a further reduction in 1947 to only 12 animal units, the graph of forage consumption was continuously lowest (Fig. 58). The very moderate consumption of forage in early spring is clearly a result of its scarcity. Seasonal trend is practically the same as in preceding years.

Monthly and annual yields and consumption are shown in Figure 60. Even casual examination shows that the yield was highest in 1945 and lowest in 1946; the third year yield was intermediate. The greatest difference occurred in May and June. This was due in part to a later and drier season in 1946, but especially to the excellent growth of little barley in 1945 and 1947. The high yields in May, 400 grams or more, followed by rapid decrease in June and still more in July, is the same for both 1945 and 1947. A slight increase in August followed by very low yields in September and October (75 grams or less) is also common to both years. But during the cold dry spring in 1946, yield in May was low (less than 200 grams). Otherwise, except for the absence of an increased yield in August, the trend of the graph is similar to that of the preceding and the following year. Yields greatly exceeded consumption in May, except in 1946 when they were about equal. It was always greater in June and, with one exception, continuously as great or greater than consumption until September. Thereafter much of the forage consumed was that produced earlier in the year.

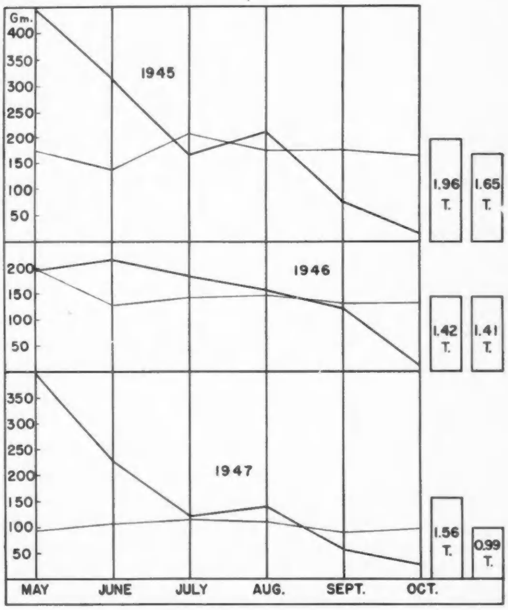

FIG. 60. Average yield (heavy lines) and average consumption (light lines) in grams per unit area each month of the growing season of 1945, 1946, and 1947. Seasonal yield and consumption are shown in tons per acre.

Seasonal yield was highest the first year, 1.96 tons per acre. The amount consumed was 1.65 tons or 84 percent of the yield. Since the south half of the pasture nearest the well was grazed very closely late in autumn, this left uneaten about 30 percent of the forage in the more distant part. Yield was so greatly reduced in the drier year, 1946, that of the 1.42 tons per acre practically all (99 percent) was consumed. This was shown by the close and even grazing everywhere in October. Of the intermediate yield, 1.56 tons per acre in 1947, the reduced herd consumed only 0.99 ton or 63 percent.

That the pasture was adequately sampled may be seen by comparing the results from the original exclosures in 1947 with a similar group of 9 new ex-

closures used here for the first time. They were placed in 9 new sampling areas as similar as possible to those sampled by the first group in 1947 but 40 to 100 yards distant. The data obtained from the two groups are shown in Table 9.

TABLE 9. Average monthly and total consumption and average monthly and total yield in grams from two similar sets of sampling areas in 1947.

Exclosures	May	June	July	Aug.	Sept.	Oct.	Total
Consumption							
First group	819	916	1,061	1,029	893	878	5,596
Second group	853	988	1,050	968	884	893	5,636
Yield							
First group	3,463	2,223	985	1,181	407	391	8,650
Second group	3,718	1,898	1,194	1,378	655	98	8,941

From the preceding data it may be concluded that the pasture was understocked the last year. About 15 animal units or 5 acres per animal unit seems to be a proper rate of stocking this excellent buffalo grass pasture provided a more equal distribution of grazing could be had. This might be attained by fencing to keep the cattle in the far end of the pasture in the morning, and the placing of salt just south of the fence where both salt and water could be had in the afternoon. Further studies now well under way will greatly increase our knowledge of this great pasture region.

The writers wish to express their gratitude to Dr. R. W. Darland who accompanied them on many field trips and assisted in other ways.

SUMMARY

A portion of the Dissected Loess Plains of central Nebraska, several thousand square miles in area, occupies a region directly southeast of the Sandhills and north of the Platte River. It extends over four large counties and includes the territory between Broken Bow and Ord on the north and Lexington, Kearney, and Grand Island on the south.

The area is developed principally on mantle rock materials of Pleistocene age. During middle and later Pleistocene time the interfluve areas received relatively thick mantles of wind-blown dust known as loess. Much of this was blown up from alluvial flats along the through valleys of the region. The Sandhills released much Tertiary and Pleistocene loess-forming material which contributed directly or indirectly to the Loveland and Peorian deposits. The aggregate thickness of the loess mantle approaches 150 feet or more in places.

Headwater erosion into the loess plain has rapidly developed the characteristic canyon topography of the region. Once the sod and thin soil cap of the upland plain is removed by undercutting, the relatively coarse silts of the loess erode rapidly.

Before the Peorian loess was deposited on it, a dark soil with a clayey subsoil was developed at the top of the Loveland loess. Water easily enters and penetrates downward through the Peorian loess often to 30 or 40 feet. At the contact with Loveland loess its further penetration is greatly restricted. Hence, the ground water movement is directed laterally toward the valley or canyon sides where water is discharged as springs and causes the overlying Peorian loess to slip or slide valleyward. Catsteps are thus developed. These are a typical feature of the side slopes of the uplands.

Average elevation of the upland plain is about 2,200 feet above sea level. Over the greater part of the area it has been thoroughly dissected. The bluffs and hills are often 100 to 150 feet higher than the valleys between them. Comparatively level areas are not extensive. Nearly all the area is well drained by streams and rivers—North, Middle, and South Loup Rivers, and Wood River—southeastward into the Platte River. Runoff is usually excessive and erosion is severe.

The climate is characterized by moderately long, cold winters and a fairly long growing season with hot summers. Annual precipitation averages about 23 inches, evaporation is high, wind movement is fairly constant and often high, and mid and late summer droughts are frequent.

The soils are constantly rejuvenated, chiefly by deposition of wind-blown dust. Well developed soils of the uplands are predominately those of the Holdrege series. The friable, dark-grayish brown silt loam is about 12 inches deep. It is underlaid by a silty clay loam subsoil to a depth of 3 or more feet. The lime layer characteristic of Chernozems occurs often between depths of 3 and 6 feet. The soil is approximately neutral in reaction.

The light-colored Colby soils, the second chief type, may be regarded as immature. Colby silt loam varies from dark grayish brown to ash-gray. The A horizon is only 4 to 12 inches deep. The subsoil or B horizon composes a part of the second foot. In many places the surface layers have been entirely removed by erosion, exposing the light, yellowish-gray parent loess.

Both soils are very fine textured. The degree of aggregation (14 to 24 percent) is very low. Organic matter is about 4 to 5 percent in the surface foot, and nitrogen 0.110 to 0.194 percent. Because of these characteristics, the soils are easily eroded and the maintenance of a cover of vegetation is important.

The grasses and forbs develop well-branched, deeply penetrating root systems. Buffalo grass penetrates to 4-6 feet, western wheat grass to 8-10 feet, and various perennial forbs to 15 feet or more in the mellow, moist loess.

Although the land was homesteaded about 1870, a third to a half of it is still under native grass. It is recommended by the U. S. Soil Conservation Service that the steeper uplands should always be protected by a cover of grass.

There were four communities or types of grassland in the mixed prairie association of these loess hills. In the short-grass type or faciation blue grama *(Bouteloua gracilis)* was far more abundant than buffalo grass *(Buchloe dactyloides)*. Buffalo grass

was often entirely absent in virgin ungrazed prairie.

Short grasses dominated in the drier portions of most prairies, usually in almost pure stands or even where there was an intermixture of taller grasses. These sites included various slopes but especially those where runoff was high. In some places blue grama was intermixed or alternated with rather extensive patches of buffalo grass. In other places, even on dry slopes, the short grasses gave way to mid grasses. The type was characterized by an overstory of hairy chess *(Bromus commutatus)*, an invader during drought.

The mid- and tall-grass type occurred typically on the lower slopes of hills and in ravines partially protected from wind and sun and where runoff water from the slopes supplemented rainfall. Where the soil had slumped to produce catsteps on the hillsides, vegetation was of much the same type. Chief species of this postclimax associes were big bluestem *(Andropogon furcatus)*, side-oats grama *(Bouteloua curtipendula)*, western wheat grass *(Agropyron smithii)*, switchgrass *(Panicum virgatum)*, and nodding wild rye *(Elymus canadensis)*.

The typical expression of the association was shown in the mixed short- and taller-grass type. This community occurred in transitional areas of considerable extent where species from the two preceding types grew more or less in equal abundance forming the characteristic layered vegetation of mixed prairie. Here big bluestem largely replaced little bluestem *(Andropogon scoparius)* which had mostly succumbed to drought. Side-oats grama and western wheat grass were often abundant. Secondary species of greatest abundance, which also occurred in preceding types, were *Muhlenbergia cuspidata, Poa pratensis, Koeleria cristata, Sporobolus cryptandrus,* and *Panicum scribnerianum*.

The western wheat grass type was present locally in many different prairies. It often covered a single ridge or valley or a particular slope. But often it dominated very extensive areas or entire prairies almost to the exclusion of other grasses. Western wheat grass spread widely when the soil was partly bared by drought. Sometimes it had an understory of blue grama, or more frequently one of hairy chess. But it usually occurred in pure stands, forming an extensive consociation. Its boundaries were mostly more distinct than those of the three preceding types which were often indefinite, and fragments of one community frequently occurred as patches or islands in the others.

About 24 principal species of forbs occurred in the several communities. *Amorpha canescens,* a half-shrub, was most abundant, conspicuous, and widely distributed. About 50 other forbs were of secondary importance. Drought had taken its toll and recovery was incomplete. Certain shrubs formed thickets bordering ravines.

The grassland has been used chiefly for grazing, largely for summer range, especially for cattle. Consequently the vegetation has undergone various changes, somewhat in proportion to the intensity of grazing. The ranges varied in size from 80 acres to a square mile or more.

The vegetation consisted chiefly of blue grama, although buffalo grass was found in moderate amounts and in old, closely grazed pastures abundantly. These occurred mostly where crop production was the chief industry. Such pastures were usually smaller and often overstocked.

Big bluestem was the chief tall pasture grass; side-oats grama was less abundant except on catsteps and steep banks. Western wheat grass occurred sparingly to abundantly. These and other taller grasses were regularly found in places favored by receiving run-off water. In general, the cover had been greatly disturbed by drought or dust coverage. Often sand dropseed *(Sporobolus cryptandrus)* was common, purple three-awn *(Aristida purpurea)* occurred on bared slopes, and hairy chess was abundant.

Under grazing, the tall and mid grasses were reduced in vigor much more rapidly than were the short grasses which had more foliage close to the soil. Grazing and drought had more or less completely removed the mid-grass layer and many species of the ground layer. The remaining species were now more widely spaced.

After long periods of close grazing and trampling, the taller grasses in the ravines, on their steep banks, and even on the catsteps, were replaced by blue grama and buffalo grass. Long continued heavy grazing was less harmful to the sod-forming buffalo grass than it was to the bunches of blue grama. Buffalo grass also recovered and spread more rapidly over ridges and bared slopes than did blue grama.

Of 29 ranges carefully examined 9 were characterized by buffalo grass and 8 by blue grama, 15 percent or less being composed of the other short grass, which ranked second. But where larger percentages of the second ranking grass were present, buffalo grass exceeded blue grama in only 3 ranges, while blue grama exceeded buffalo grass in 7.

Grazing was light, moderate, or none in 18 pastures; only 9 were overgrazed. The average basal cover usually ranged between 30 to 60 percent in the poorer parts of the range and 40 to 90 in the better portions.

The most abundant weedy annual grasses were little barley *(Hordeum pusillum)*, six-weeks fescue *(Festuca octoflora hirtella)*, and hairy chess. Where abundant, little barley furnished much forage in spring. Hairy chess, common in nearly all ranges, has a high forage value in spring and early summer.

About 30 species of native forbs were found to occur widely and often abundantly. They provided a valuable variety in the diet of livestock grazing native ranges.

Chief introduced weeds were hoary vervain *(Verbena stricta)*, prostrate vervain *(V. bracteosa)*, and horseweed *(Leptilon candense)*. Horseweed was

eaten when young but often grew so thickly that later it hindered uniform grazing.

Two pastures near Kearney were selected for a study of the monthly and annual yield and consumption of forage. The seasonal grazing patterns varied mostly with the type of vegetation available to the livestock, its period of development, and, consequently its palatability. They also varied with the grazing pressure.

Monthly consumption of forage was ascertained in 3 or 4 sampling areas in each grazing type. This was accomplished by clipping the forage close to the soil at the end of each month in 30-square-foot portable exclosures and in adjacent grazed areas of a similar size. The air-dry weight of the first lot of forage minus that which was uneaten in the adjacent area equaled the amount consumed. New locations were used each month.

Yield was ascertained each month by subtracting from the dry-weight of the forage in an exclosure at the end of the month the dry-weight of the approximate amount that occurred there at the beginning of the month.

During 1945, a year favorable for growth, 55 animal units of cattle consumed 1.86 tons of forage per acre in the buffalo grass-bluegrass type on the lowlands. Annual consumption in the buffalo grass type on the hillsides was 1.30 tons. In the more open sand dropseed-buffalo grass type on hilltops only 1.03 tons of forage were consumed, and in the seral type dominated by three-awn grasses only 0.57 ton of forage was eaten. This pasture was 160 acres in extent, but almost half of it was a 23-year-old subsere following breaking.

During the drier year which followed, a reduced herd of 36 animal units consumed 1.78 tons of a 2.19 tons yield on the lowlands. In the buffalo grass type, yield was 1.26 tons and consumption 1.03. The sand dropseed-buffalo grass type yielded 0.98 ton; 0.71 ton was consumed. In the subsere, yield and consumption were 0.71 and 0.24 ton, respectively.

The second pasture consisted of 70 acres of excellent, almost pure buffalo grass. Grazing patterns during the three years 1945 to 1947 inclusive, varied with lateness of spring and especially with precipitation. Yield, as in the preceding pasture, exceeded consumption in spring and early summer, but it was usually exceeded by consumption after August. Here 18 sampling areas were used.

The first year 18 animal units consumed 1.65 tons of forage per acre of the 1.96 tons yield. The next year, which was less favorable for growth, 17 animal units consumed 99 percent of the 1.42 tons yield per acre. The third year, which was more favorable for growth, 12 animal units consumed 0.99 ton per acre of the 1.56 tons yield.

Thus, under good management, a stocking rate of about 15 animal units or approximately 5 acres per animal unit seems to be a proper one in this excellent buffalo grass pasture which is typical of many others throughout these loess hills.

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